

UNIVERSIDADE DE SÃO PAULO
FACULDADE DE FILOSOFIA, CIÊNCIAS E LETRAS DE RIBEIRÃO PRETO
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA COMPARADA

Characterization of macroevolutionary patterns of body size in Testudinata
Caracterização dos padrões macroevolutivos do tamanho corporal em Testudinata

Bruna de Mattos Farina

Dissertação apresentada à Faculdade de Filosofia,
Ciências e Letras de Ribeirão Preto da
Universidade de São Paulo, como parte das
exigências para obtenção do título de Mestre em
Ciências, obtido no Programa de Pós-Graduação
em Biologia Comparada

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Orientador: Prof. Dr. Max Cardoso Langer

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[...] A gente vive repetido, o repetido, e, escorregável, num mim minuto, já está empurrado noutra galho. Acertasse eu com o que depois sabendo fiquei, para de lá de tantos assombros...um está sempre no escuro, só no último derradeiro é que clareiam a sala. Digo: o real não está na saída nem na chagada: ele se dispões para a gente é no meio da travessia. [...]

– João Guimarães Rosa, em “Grande Sertão: Veredas”

Resumo

Organismos, sejam eles vertebrados ou invertebrados, apresentam uma grande variedade de tamanhos e formas. A explicação para isso, entretanto, sempre foi conturbada, e diversas hipóteses, incluindo tanto tendências intrínsecas, quanto extrínsecas (e.g., termorregulação), foram propostas para explicar tais variações. Nesse contexto, os Testudinata apresentam grande disparidade de tamanhos corpóreos, especialmente se levado em conta o seu rico registro fóssil. No presente trabalho, foi explorada a evolução do tamanho corpóreo no grupo, analisando fatores relacionados aos padrões encontrados e a possível presença de tendências evolutivas (e.g., Lei de Cope). Para tal, duas superárvores foram construídas e calibradas no tempo geológico, baseadas em duas hipóteses filogenéticas independentes, e foram coletados dados de tamanho corpóreo, bem como outras informações como habitat e idade de cada táxon. Para a análise dos dados, foram realizadas regressão linear entre paleotemperatura e tamanho corpóreo, reconstrução de estados ancestrais, ajuste a diferentes modelos evolutivos, além da análise dos dados de tamanho ao longo do tempo. Os resultados obtidos indicam que não há um padrão geral que explique o tamanho das tartarugas ao longo do tempo; pelo contrário, tartarugas de diferentes hábitos ecológicos e diferentes linhagens apresentam padrões diferentes de variação de tamanho. Enquanto tartarugas de água doce apresentam pouca variação de disparidade ao longo tempo, possivelmente relacionada com os diferentes fatores ambientais característicos dos mais variados ambientes dulcícolas, tartarugas terrestres e marinhas apresentam grande variação, sendo o tamanho das terrestres possivelmente relacionado com certas condições ambientais e colonização de ilhas, e o das marinhas com adaptações para o ambiente pelágico, o que possibilitou maior dispersão do grupo. Mesmo tendo sido observada uma possível tendência de aumento ou

diminuição de tamanho em certas linhagens, isso não foi confirmado pelos modelos evolutivos ajustados.

Abstract

Organisms, vertebrates or invertebrates, display an amazing variation of body size and shape. The explanation for that, however, has always been debated, and different hypotheses, including trends of body size and thermoregulation, were proposed to explain this variation. In this sense, Testudinata shows great disparity of body size, especially if its rich fossil record is accounted. In this study, I explore the body size evolution in turtles, analyzing which factors could influence the observed patterns, and the presence of long-term evolutionary trends (e.g., Cope's Rule). For this, I constructed and time-calibrated two supertrees, based on two independent phylogenetic hypotheses, and collected body size data, as well as habitat information and age for each sampled taxon. To analyze body size data through time, I performed linear regression between paleotemperature and body size, ancestral state reconstructions, and macroevolutionary models fitting. The results suggest there is no general pattern that explains body size evolution in the group; instead, different habitats and lineages show different patterns of body size variation. Whereas freshwater turtles display a homogenous body size variation through time, possibly related to the uneven environmental factors of these habitats, terrestrial and marine turtles show more pronounced variation. Terrestrial turtles body size is likely related to environmental conditions and island colonization, and that of sea turtles to their pelagic lifestyle, which allowed great dispersal. Even though a few groups seemed to show some trends of body size, the evolutionary models indicate the opposite.

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Introduction

Body size, evolutionary trends, and thermoregulation hypotheses

During the ~3.6 Ga of life's history on Earth, organisms evolved great disparity of body plans, mass, sizes, and functions (Smith, et al., 2016). Because body size has several implications in an organisms' life, from physiology to ecology, the topic has always intrigued researchers and its role in micro and macroevolution — acquisition of a new trait or production of ecological opportunities — has been extensively debated (Schmidt-Nielsen, 1984; Peters, 1986; Maurer, Brown, & Rusler, 1992; Blanckenhorn, 2000). The relationship between phenotypic evolution and diversification of organisms is also a widely discussed issue in evolutionary biology (Cooney & Thomas, 2021).

The evolution of body size is commonly explained in the light of different hypotheses that attempted to elucidate patterns of disparity in different clades, such as the Cope — tendency of a lineage to evolve towards larger body size (Cope, 1896; Benton, 2002) —, Bergman — tendency of having larger sizes in cooler regions (Bergmann, 1847) —, and Rensch — tendency to sexual size dimorphism increasing when males are already larger than females or the opposite (Rensch, 1950) — rules. Specifically, Cope's rule is somewhat puzzling, since there is no apparent need for selection to produce ever larger body sizes (Gould, 1988). There is, however, favorable evidence for this rule (e.g., Alroy, 1998; Laurin, 2004; Heim et al., 2015; Benson et al., 2018), as well as against it (Laurin, 2004; Moen, 2006, Godoy et al., 2019).

Besides evolutionary trends over time, several hypotheses regarding heat conservation try to explain body size variation (Rodrigues et al., 2018). In this sense, ectotherms — animals without physiological mechanisms for heat production and retention (Davenport, 1992) — are expected to have an intrinsic relationship to environmental temperature, which could influence their growth rates and body size

(Davenport, 1992; Atkinson, 1994; Angilletta et al., 2004). It is expected that ectotherms will present slower growth rates in lower temperatures, but reaching larger body sizes in a long term, and the opposite in higher temperatures (Davenport, 1992; Atkinson, 1994; Partridge & French, 1996). Even with different variables, such as food resources or competition, in different areas, temperature seems to have major roles in the size attained by some species (Partridge & French, 1996). Nevertheless, this once widespread idea has been recently challenged, because some groups do not follow this relationship (Davenport, 1992; Rodrigues et al., 2018).

Gigantothermic organisms use large body sizes, low metabolic rates, peripheral tissues, and circulatory changes to maintain high body temperature in cold environments and avoid overheating in warm temperatures (Paladino et al., 1990). This kind of thermoregulation occurs because large animals present larger thermal inertia than smaller ones, due to a smaller surface area/body volume relationship, reducing heat loss to the environment (Spotila et al., 1993). This relationship has been demonstrated for different groups, such as large crocodiles, dinosaurs, and also large turtles (Paladino et al., 1990; Spotila et al., 1993; Seebacher et al., 1999; Seymour, 2013). However, specifically about turtles (Testudinata), the few studies about the evolution of body size in the group frequently ignore their unusually rich fossil record (e.g., Moen, 2006; Jaffe et al., 2011; Eastman et al., 2011; Uyeda & Harmon, 2014) or are limited to less inclusive groups (e.g., Vlachos & Rabi, 2018).

Turtles and their morphological disparity

Testudinata has a rich fossil record and relatively stable phylogenetic relationships, which provides a reliable framework for macroevolutionary studies, making the group an excellent study system for trait evolution, such as body size (Finarelli & Flynn, 2006;

Fritz et al., 2013). The crown-group Testudines (i.e., modern turtles) includes 356 living species (TTWG, 2017), but its fossil record, and that of its total-group Testudinata, reveals a much more diverse history (Gaffney et al., 2006; Joyce et al., 2013). The early evolution of Testudinata is thought to have occurred in terrestrial habitats (Joyce & Gauthier, 2004; Joyce, 2017; Lautenschlager et al., 2018), but Testudines likely diversified later in aquatic environments (Joyce & Gauthier, 2004, Joyce, 2017). Nowadays, the two main extant lineages, Cryptodira and Pleurodira, occupy a diverse range of habitats. Cryptodira (“hidden-necked turtles”) is the more diverse of the two and its species typically occur in temperate and tropical regions of all continents (with the exception of Antarctica). Most species are freshwater, but one extant lineage is highly adapted to a marine life (Chelonioidea) and some taxa (e.g., Testudinidae) invaded terrestrial and arid habitats (Bour, 2008). On the other hand, the members of the other main lineage, Pleurodira (“side-necked turtles”), are currently restricted to the southern hemisphere and occur exclusively in freshwater environments (Gaffney et al., 2006). The distinct habitats in which turtles can be found (de la Fuente et al., 2014; Foth et al., 2017; Ferreira et al., 2018), imposed a wide range of selective pressures along the evolution of the group. This is reflected, among other factors, in the great morphological disparity of their limbs, skull, carapace shape, and body size (Joyce & Gauthier, 2004; Benson et al., 2011; Jaffe et al., 2011; Foth et al., 2017; Vlachos & Rabi, 2018; Lautenschlager et al., 2018; Dickson & Pierce, 2019).

Considering the relatively small diversity of the group (in comparison to mammals, birds, and squamates), the body size disparity of turtles is striking. The smallest living testudine, *Homopus signatus*, has a carapace length of about 10 cm, and the largest one, *Dermochelys coriacea*, reaches more than 1.5 m (Bonin et al., 2006). Furthermore, fossils display an even broader range of body sizes, including the South American *Stupendemys*

geographicus, with a carapace length of more than 2.8 m (Cadena, et al., 2020), and *Kinosternon pojoaque*, from North America, with 8.5 cm (Bourque, 2012). This reinforces the importance of including the majority of the fossil diversity when characterizing the patterns of body size evolution in Testudinata, which all of the previous attempts failed in doing (Moen, 2006; Jaffe et al., 2011; Eastman et al., 2011; Uyeda & Harmon, 2014; Vlachos & Rabi, 2018).

Focusing mostly on the recent diversity, previous works have elaborated hypotheses to explain the observed body size variation in the group. For example, body size variation in turtles is thought to be intrinsically related to their habitat, with marine species and island tortoises usually possessing larger sizes than freshwater and mainland taxa (Jaffe et al., 2011). Similar patterns have been found for other groups, such as some mammals, reptiles, and birds (Lomolino, 2005), but for turtles this claim has been challenged and is not yet consensual (e.g., Uyeda & Harmon, 2014). At the same time, an analysis of body size focused on Testudinidae (Vlachos & Rabi, 2018) did not find support for the insular effect. Moreover, Moen (2006) tested for evolutionary trends in extant cryptodires but found no support to Cope's rule (Moen, 2006). Nevertheless, such claims have yet to be tested in a framework including both extinct and extant taxa. In the present study, the largest body size dataset ever assembled to Testudinata is used to investigate this and other important questions related to the evolution of body size in the group.

Aims

Here, I aim to characterize the evolutionary patterns of body size in turtles (Testudinata), by compiling a comprehensive body size dataset, with extensive sampling of living and extinct taxa. I use through-time plots, ancestral state reconstructions, correlation tests, and model-fitting analyses to investigate the relationship between body size and different

biotic and abiotic factors, such as geological time, ecological groups, and paleotemperature. The large sample analyzed here also allowed me to provide more reliable ancestral body size estimates. My main goal in this study was to answer the following questions:

1. What are the deep-time patterns of body size evolution in turtles when the fossil record is considered?
2. Do estimates of ancestral body sizes change when extinct species are included?
3. Do species of different ecological habitats show distinct body size through time patterns?
4. Can body size evolution in turtles be explained by habitat choice or paleotemperature?
5. Do turtles follow the Cope's rule or other general evolutionary rule?

Methods

Supertree construction and time-calibration

I manually constructed two informal supertrees using Mesquite version 3.61 (Maddison & Maddison, 2019) for employing the subsequent phylogenetic comparative methods. The relationships among major groups within Testudinata were based on two phylogenetic hypotheses: Evers et al. (2019) and Sterli et al. (2018), hereafter referred to as “Ev19” and “St18”, respectively. Less inclusive groups were positioned based on several hypotheses (Appendix 1). Each supertree – “Ev19” and “St18” – included a total of 846 taxa, resulting in a considerable expansion in relation to similar previous studies (Jaffe et al., 2011 = 226 taxa; Angielczyk et al., 2015 = 245 taxa; Vlachos & Rabi, 2018 = 59 taxa, Moen, 2006 = 201 taxa).

The most significant differences between the two supertrees are the positions of Protostegidae and Thalassochelyidia (sensu Joyce et al., 2021). Protostegids are stem-Chelonioidea and Thalassochelyidia are stem-Pleurodira in “Ev19”, whereas in “St18’s” (in which they are originally represented only by *Santanachelys gaffneyi* and *Solnhofia parsoni*, respectively; Sterli et al., 2018) both are within the stem-lineage to Testudines. A complete description of the supertree construction can be found on Appendix 1.

Both supertrees were time-scaled using Bayesian inference under a Fossilized Birth-Death (FBD) model, performed with MrBayes version 3.2.7 (Huelsenbeck & Ronquist, 2001). The FBD process acts as a prior for estimating divergence times and provides an explicit speciation-extinction-fossilization model to explain diversification (Stadler, 2010; Heath et al., 2014). Even when its assumptions are violated by the data — for example, by artifacts of fossil preservation and sample biases, which were significant caveats in earlier methods (e.g., Felsenstein, 2002; Pyron, 2011; Ronquist et al., 2012) —, the model still provides reliable and robust node age estimates (Heath, Huelsenbeck, & Stadler, 2014).

I used R (version 4.0.2; R Core Team, 2020) package *paleotree* (Bapst, 2012) to create a MrBayes command for time-calibration analyses — all functions and analyses performed using R can be found in Appendix 2. The function *createMrBayesTipDatingNexus()* allows the use of “empty” morphological matrices in clock-less tip-dating analyses (Bapst & Wagner, 2019). The two supertrees (“Ev19” and “St18”) were entered as topological constraints (i.e., for two separate time-scaling analyses) and data on occurrence times (= tip ages) were obtained from the primary literature and supplemented by the Paleobiology Database (PBDB). Four taxa formed the outgroup (*Eunotosaurus africanus*, *Eorhynchochelys sinensis*, *Pappochelys rosinae*, and *Odontochelys semitestacea*) and, based on their age (as well as that of the oldest turtles),

the root of the tree was defined, using a uniform distribution, between the Kungurian and the Roadian stages of the Permian (283.5 and 268.8 Ma), as this would represent a maximum possible age for the origin of the group. Two runs of MCMC analyses, with four chains each, were set for 20,000,000 generations, with 25% burn-in. Convergence of both runs were verified when values of potential scale reduction factors approached 1.0 and average standard deviation of split frequencies was below 0.01.

Body size data collection

Straight-line maximum dorsal carapace length (MCL) was taken as a proxy for turtle body size (as in Jaffe et al., 2011). Aiming to maximize sampling, I also used linear regressions to estimate total carapace length from ventral skull length (measured from premaxillae to the occipital condyle) for some specimens in which carapaces were not preserved (Appendix 3). The estimated data represents about 7.5% of the entire dataset. Measurements were collected from photographs (personal archive or the literature) using the software ImageJ (Schneider et al., 2012). I collected body size data for 659 out of the 846 taxa included in the supertree. I also collected information about preferable habitat and chronostratigraphic provenance for all taxa included in the body size dataset (see Appendix 3). In addition to the 659 taxa included on the tree for which body size data is available, I also collected MCL, ecological and chronostratigraphical data for 136 additional species not included in the supertree, resulting in a total sample of 795 taxa which were included in some of the subsequent macroevolutionary analyses not requiring phylogenetic information.

Body size analyses

Phylogenetic comparative methods

In order to characterize the body size evolution of turtles, I used maximum likelihood to estimate the ancestral states (= ancestral body sizes) under Brownian motion, using the R package *phytools* (Revell, 2012). Ancestral state reconstructions were performed with both the complete supertree (i.e., with fossils and extant specimens) and with a subset tree of extant taxa only (= reduced dataset).

In order to test if Cope's rule plays an important role in turtle body size evolution, I fitted different macroevolutionary models to both supertrees topologies (i.e., "Ev19" and "St18"). To account for temporal and phylogenetic uncertainties, I ran the model-fitting analyses using 10 time-scaled versions of "Ev19" and 5 time-scaled versions of "St18" (the limited number of trees of the "St18" topology are due to time constraints).

Firstly, I fitted a set of uniform phenotypic models: Brownian Motion (BM), Early Burst (EB), evolutionary "trend" and Ornstein-Uhlenbeck (OU). The BM, initially proposed by Felsenstein (1985), assumes a stochastic dispersion process, with constant evolution for each given character (Felsenstein, 1985; Freckleton & Harvey, 2006), and is very useful to model processes of random genetic drift and rapid adaptation to fluctuating environment (Felsenstein, 2004). The model has two parameters: sigma square (σ^2), which indicates evolutionary rate, and the root state of the trait at time zero, sometimes represented by $X(0)$ (Cooper et al., 2016). Moreover, modifications of BM, such as the "trend" model, incorporates a bias (β) that allows detection of directional trends along branches (Pagel, 2002). In the context of the present study, the "trend" model would be the representation of the Cope's rule, given that this "rule" is described as a multi-lineage directional trend towards larger sizes. Another modification of BM, OU process incorporates a trait optimum (θ) towards which the character values are attracted.

The strength of this attraction is represented by the alpha parameter (α) (Butler & King, 2004; Jaffe et al., 2011). Lastly, in the EB model, lineages experience a burst of rapid increase in trait variation in the beginning of their evolutionary history, followed by a deceleration (Harmon et al., 2010).

Additionally, I also fitted 13 non-uniform (i.e., multi-regime) trend-like models using the script of Benson et al. (2018). As with the uniform “trend” model, these multi-regime trend-like models incorporate directional trends in the analyses to test for the presence of Cope’s rule. However, unlike the uniform version, non-uniform trend-like models allow the μ parameter — the amount of directional change in a trait through time (Pagel 2002; Hunt & Carrano, 2010) — to vary along the tree in temporal or node shifts (time shift model and node shift model, respectively). I fitted three time-shift (which allow shifts in all branches after a determined point in time) and ten node-shift models (which allow shifts in specific branches). All fitted models (i.e., BM, EM, uniform trend, OU, and multi-trend) were compared using Akaike’s information criterion for finite sample sizes (AICc) for the selection of the best fit.

Through-time and between group variation

I plotted body size data (using the total matrix of 795 taxa) through time and used Welch Two Sample t-test (Welch, 1947) to assess significant mean changes across different time intervals and ecological categories. In order to test if body size is related to paleotemperature, I also tested correlations between those variables using Generalized Least Squares (GLS) and Ordinary Least Squares (OLS). The GLS regressions were used to incorporate a first-order autoregressive model which accounts for potential inflation of correlation coefficients created by temporal autocorrelation. I used two different paleotemperature curves: from Zachos et al. (2008), which compiled information about

foraminifer isotopic ratios from the Maastrichtian to Recent; and Prokoph et al. (2008), that assembled isotopic information from marine carbonates, from the Precambrian to Recent, but with significant gaps in the time series. Using the R package *dispRity* (Guillerme, 2018), I partitioned the data into time bins, using chronostratigraphic stages, as well as equally spaced intervals of 10 and 5 Ma. I analyzed the complete dataset (e.g., all turtles), as well as Pleurodira and Cryptodira subsets.

It is important to note that I divided the carapace measurements in quartiles, in order to be more precise when exposing the results. Thus, MCLs ranging from 8.45 cm to 20 cm were considered small; from 20.1 cm to 47.5 cm were considered medium size; from 47.9 cm to 110 cm are large; and 113 cm to 267 cm were considered giant.

Results

Time-calibrated supertrees

Even though I used two different topologies (Figure 1 e 2), the time-scaled supertrees show, in general, similar median age for all the groups (Appendix 4). Moreover, none of the trees presents a clear pattern of older or newer node estimates; on the contrary, 95% highest posterior density (HPD) age ranges and median ages varied unevenly among the groups.

The analysis placed the origin of turtles — Testudinata — between 253.06 and 229.08 Ma in “Ev19” and between 248.85 and 229.28 Ma in “St18”. With such similar results, the median age is 241.02 and 239.86 Ma in “Ev19” and “St18”, respectively. Likewise, the estimates for Testudines, Pleurodira, and Cryptodira also presented similar node ages in both supertrees. The divergence of Testudines occurred at 186.49 Ma (95% HPD range = 192.15 to 176.01 Ma) in “Ev19”, and at 183.09 Ma (95% HPD range = 197.44 to 170.79 Ma) in “St18”. Pleurodira origin happened at 150.50 Ma (95% HPD

range = 159.44 to 136.87 Ma) in “Ev19”, and at 152.23 Ma (95% HPD range between 172.27 and 137.56 Ma) in “St18”. The divergence of Cryptodira occurred at 170.55 Ma (95% HPD range between 186.77 and 156.78 Ma) in “Ev19”, and at 166.97 Ma (95% HPD range = 184.48 to 152.55 Ma) in “St18”.

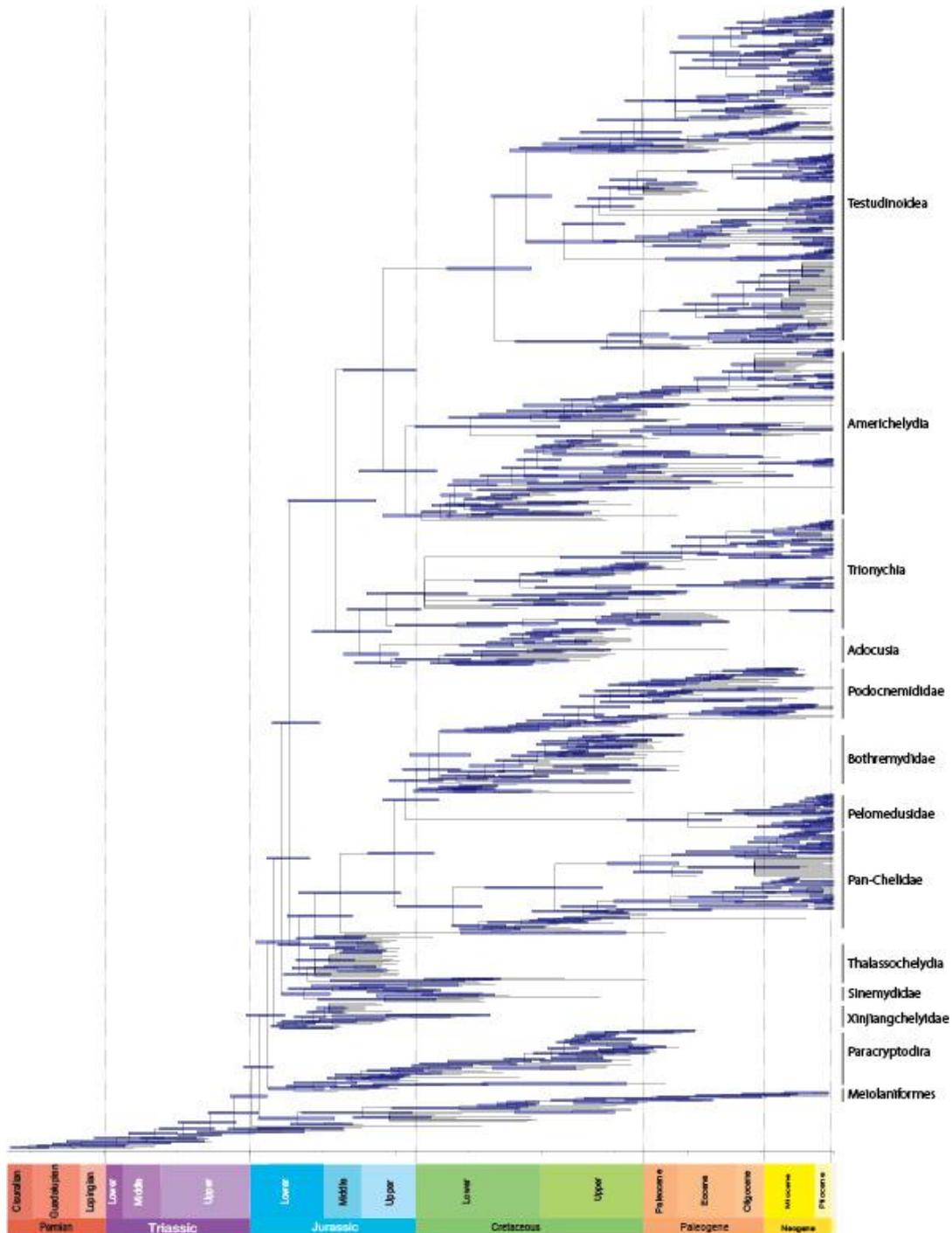


Figure 1. The “Ev19” time-calibrated supertree. Blue bars represent the 95% highest posterior density (HPD) age ranges for each node.

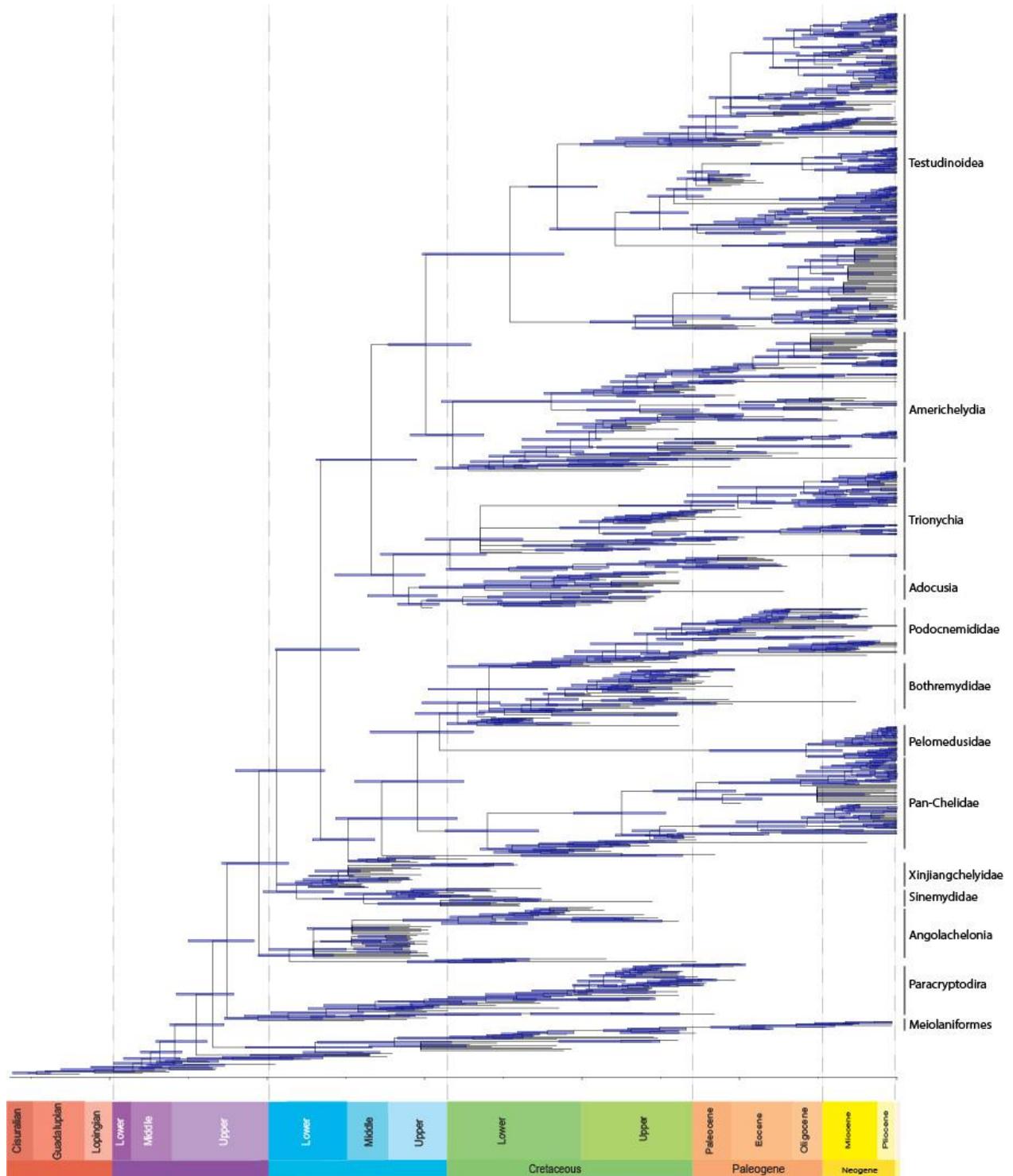


Figure 2. The “St18” time-calibrated supertree. Blue bars represent the 95% highest posterior density (HPD) age ranges for each node.

Instead, other groups, such as Perichelydia, Paracryptodira, and Pelomedusidae, presented quite different node ages between both topologies. The divergence of Perichelydia, according to “Ev19”, occurred at 196.49 Ma (95% HPD range between

206.57 and 193.97 Ma), but at 217.42 Ma when using “St18” (95% HPD range between 228.90 and 210.65 Ma). The divergence of Paracryptodira occurred at 184.73 Ma (95% HPD range between 193.62 and 174.54 Ma) in “Ev19”, and at 202.93 Ma (95% HPD range between 207.27 and 182.45 Ma) in “St18”. Finally, the divergence time estimated for Pelomedusidae is 49.85 Ma in “Ev19” (95% HPD range = 207.27 to 182.45 Ma), and 28.85 Ma in “St18” (95% HPD range = 207.27 to 182.45 Ma).

Body size patterns through time

General patterns

Plots of log-transformed maximum dorsal carapace length (MCL) through time (Figures 3 and 4) show a rather constant occupation of the turtle body size space. The oldest testudinales had the highest log-MCL means (Figure 3a), with values ranging from 37.5 (*Proterochersis robusta*) to 67 (*Proganochelys quenstedtii*) cm of carapace length. The Jurassic period witnessed a significant decline (p-value = 0.001362; Table 1) in mean body size, with both the largest and smallest turtles presenting lower MCLs than those in the Triassic — 61.9 (*Thalassemys hugii*) and 13.5 (*Sichuanchelys chowi*) cm, respectively. The mean body size drops again in the Early Cretaceous (although not significantly; p-value = 0.4966; Table 1); the disparity (=range of body sizes), on the other hand, increases considerably (Figure 3). Maximum MCL reaches 158.1 cm (*Sandownia harrisi*), whereas the smallest turtle (*Caririemyx violeatae*) had 9.69 cm of carapace length. Another significant shift in turtle body size is seen between the Early and the Late Cretaceous (p-value = 0.001828; Table 1), in which mean body size increases to 36.8 cm. Contrary to the Jurassic-Early Cretaceous transition, the total body size disparity is maintained between the Early and Late Cretaceous, but there is a range shift towards larger body sizes (Figure 3a). *Archelon ischyros* reached the maximum Late Cretaceous

MCL (220.0 cm), whereas *Rhinochelys nammorensis* had the smallest (12.2 cm). Finally, no significant change in body size was detected between the Late Cretaceous and the Paleogene (mean body size = 34.9 cm, p-value = 0.4907; Table 1), the Paleogene and the Neogene (mean body size = 30.9 cm, p-value = 0.2553; Table 1), and the Neogene and the Quaternary (mean body size = 33.3 cm, p-value = 0.4457; Table 1). The maximum body sizes throughout the Cenozoic are considered giant turtles (Paleogene: *Puentemys mushaisaensis*, 164.4 cm; Neogene: *Stupendemys geographicus*, 267.4 cm; Quaternary: *Dermochelys coriacea*, 244.0 cm), and the minimum body sizes remain similar (Paleogene: *Baptemys nanus*, 90.3 cm; Neogene: *Kinosternon pojoaque*, 84.5 cm; Quaternary: *Homopus signatus* 10.3 cm). This result is consistent with the origin and diversification of extant lineages, which occupy a wide range of body sizes, including small-bodied turtles (e.g., Kinosternidae, Pelomedusidae, Chelidae, and most Testudinoidea; Figure 3).

Table 1. t-test results comparing time bins

	Triassic	Jurassic	E. Cret.	L. Cret.	Paleogene	Neogene
p-value	0.001362	0.4966	0.001828	0.4907	0.2553	0.4457
	(Jurassic)	(E. Cret.)	(L. Cret.)	(Paleogene)	(Neogene)	(Quaternary)

According to my size categorization, of the five Triassic taxa included in the dataset, two were considered large (*Proganochelys quenstedtii* and *Proterochersis porebensis*), whereas all the others are medium-sized turtles (Figure 3b). During the Jurassic, medium-sized turtles represent 68.89% of the variation, whereas 20% were small, and 11.11% large (Table 2). The Early Cretaceous shows the first giant turtles, which represent 2.44% of the diversity, but most turtles were classified as small (41.46%). This high proportion of small-bodied turtles is not repeated after this time bin, when small turtles account for

less than 27.27% (Neogene) of the total diversity (Table 2; Figure 3b). The proportions of medium- and large-sized taxa remain similar from the Late Cretaceous until the Quaternary, whereas the “giant turtles” category shows a steady increase during the same period (Table 2).

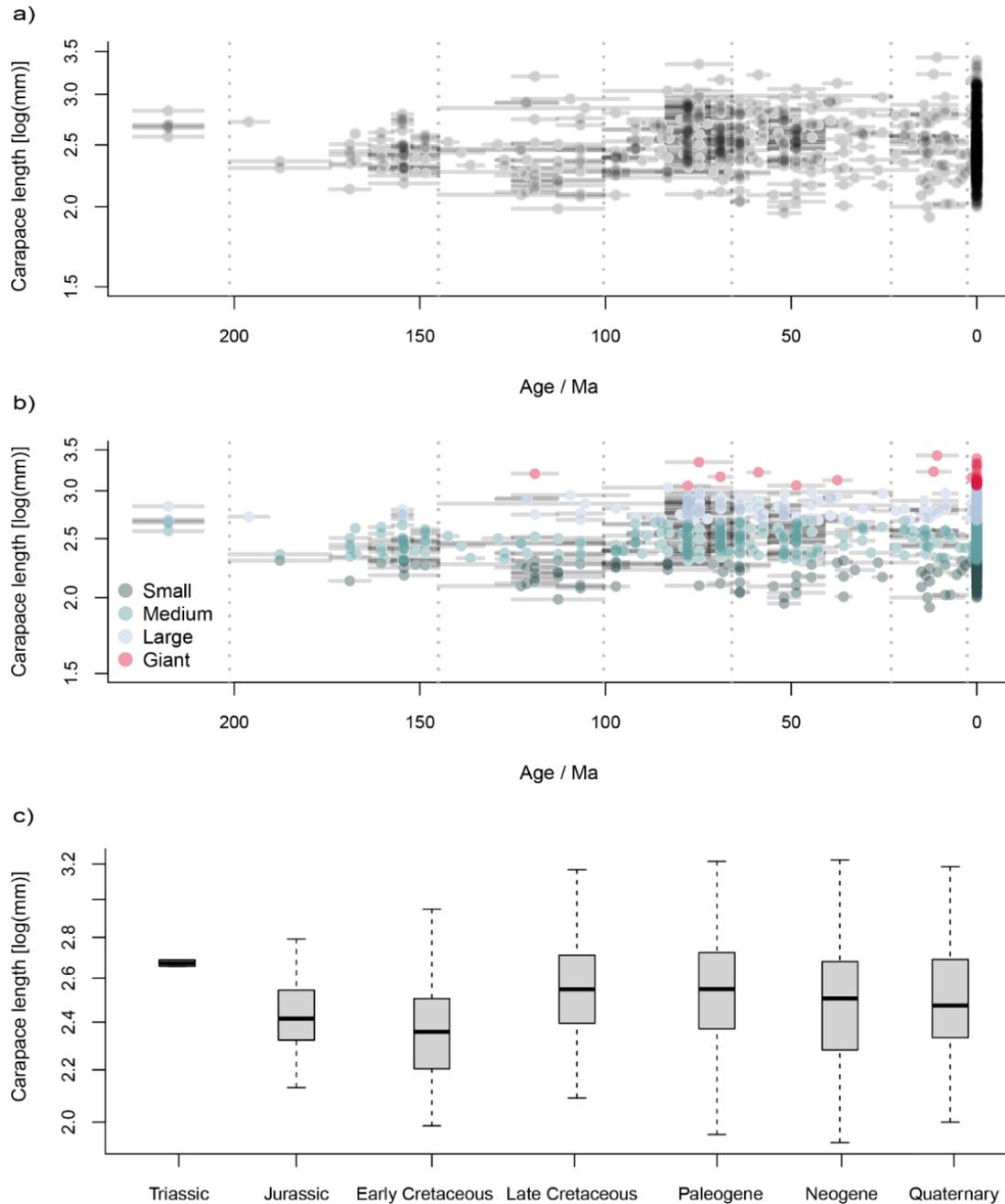


Figure 3. a) Temporal distribution of body sizes in turtles. Horizontal gray segments represent the range of occurrences of each taxon and the gray circles represent the mean age for each turtle taxon. Vertical dotted lines indicate temporal boundaries (Triassic to Jurassic; Jurassic to Early Cretaceous; Early to Late Cretaceous; Late Cretaceous to Paleogene; Paleogene to Neogene; and Neogene to Quaternary); b) Temporal distribution of body size divided into body size categories (small, medium, large, and giant); c) Box-plot showing body size values of testudinales divided into time intervals.

Table 2. Percentage of turtles in each size category per time bin.

	Small	Medium	Large	Giant
Triassic	0.00%	40.00%	60.00%	0.00%
Jurassic	20.00%	68.89%	11.11%	0.00%
Early Cretaceous	41.46%	39.01%	17.07%	2.44%
Late Cretaceous	11.67%	58.33%	27.50%	2.50%
Paleogene	17.65%	52.10%	27.73%	2.52%
Neogene	27.27%	47.27%	21.82%	3.64%
Quaternary	22.19%	50.97%	21.22%	5.61%

Differences among ecological habitats

When I analyzed the data partitioned by habitat, distinct signals were detected. Freshwater turtles seem to be the most influential group to the general curve (they also become the most common habitat category from the Jurassic onwards), with no significant changes observed in disparity and mean body size since the Late Cretaceous (Figure 4b, d). A significant increase in mean body size of turtles in this habitat (p -value = 0.001146; Table 4) was identified in the passage from the Early (23.4 cm) to the Late Cretaceous (34.6 cm). Freshwater turtles are more frequently represented among the smallest ranges, but more rarely among the largest (Figure 4b).

Diversity in terrestrial turtles is low until the Paleogene, when the first testudinids appear in the fossil record (Figure 4a). The mean body size of the terrestrial group is consistently larger than that of freshwater turtles, except during the Neogene (Figure 4d). From the Triassic to the Late Cretaceous, however, the body size disparity is low (which is expected, given the low number of species), being mostly represented by medium or large-bodied turtles (Figure 4a). The diversification of testudinids introduce a larger range of body sizes in the terrestrial category during the transition from the Neogene to the

Quaternary. They also experienced a significant increase in mean body size (from 27.2 to 44.3 cm; p -value = 0.02865; Table 3).

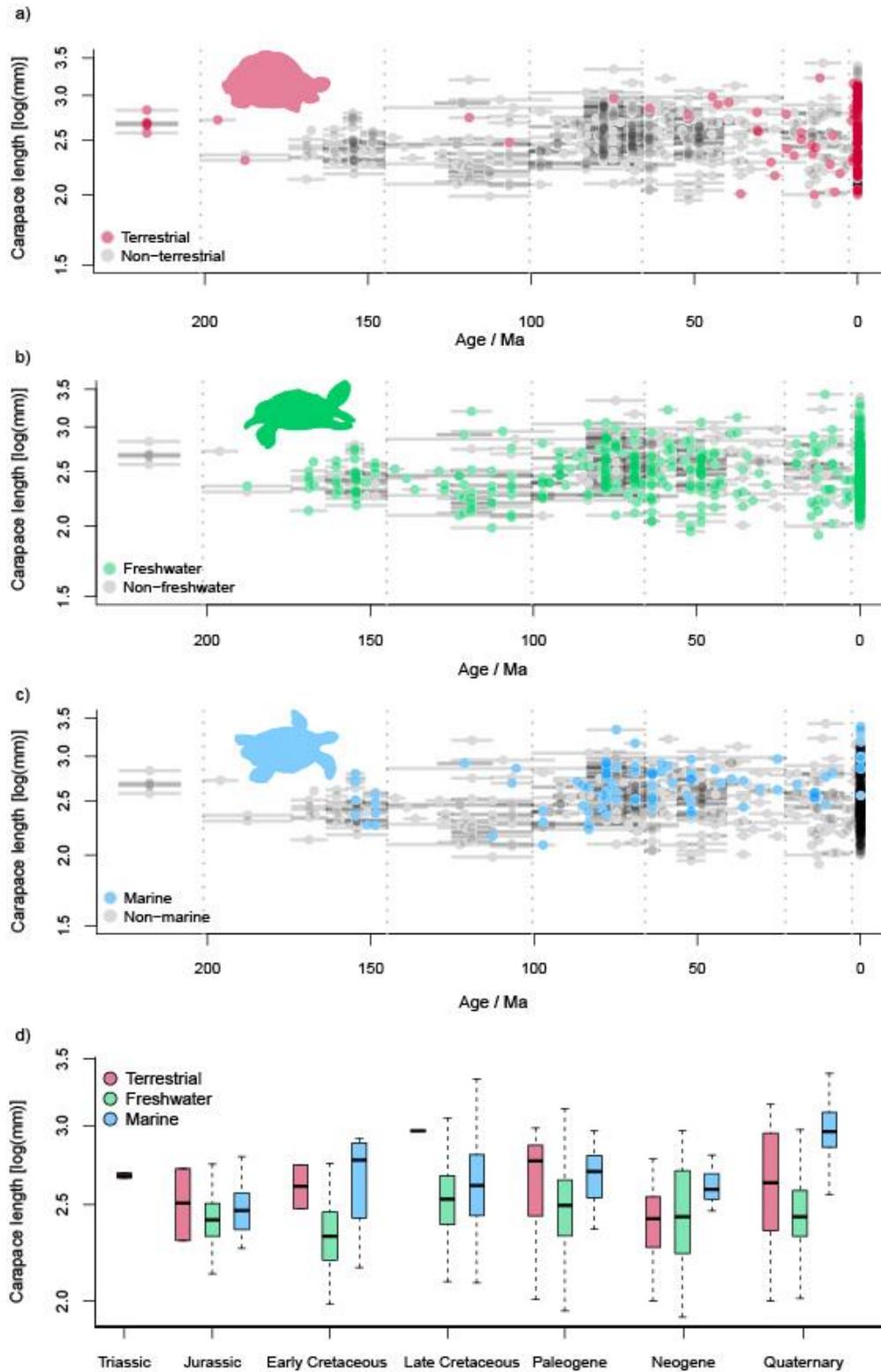


Figure 4. Temporal distribution of body sizes in turtles for different ecological habitats. Gray dots represent all taxa, whereas colored dots represent taxa subdivided into three ecological categories. a) terrestrial taxa (red dots); b) freshwater taxa (light green dots); c) and marine taxa (light blue dots). Horizontal gray segments represent the range of occurrence of each taxon. Vertical dotted lines indicate the same temporal boundaries, as in Fig.1. d) Box-plot showing body size of different ecological categories divided into time intervals. Silhouettes adapted from Jaffe, Slater, & Alfaro (2011)

Table 3. Results of t-test comparing time bins per habitats.

Marine turtles						
	Triassic	Jurassic	E. Cret.	L. Cret.	Peleogene	Neogene
p-value	-	0.3872 (E. Cret)	0.8977 (L. Cret)	0.3924 (Paleogene)	0.2409 (Neogene)	0.003958 (Quaternary)
Freshwater turtles						
	Triassic	Jurassic	E. Cret.	L. Cret.	Peleogene	Neogene
p-value	-	0.2381 (E. Cret.)	0.001146 (L. Cret.)	0.1539 (Paleogene)	0.9536 (Neogene)	0.7176 (Quaternary)
Terrestrial turtles						
	Triassic	Jurassic	E. Cret.	L. Cret.	Peleogene	Neogene
p-value	0.5516 (Jurassic)	0.7291 (E. Cret.)	0.9423 (Paleogene)	-	0.1644 (Neogene)	0.02864 (Quaternary)

The first marine taxa appear at the end of the Jurassic, with sizes similar to that of other groups (Figure 4c). There is a noteworthy (although not significant; p-value = 0.3872; Table 3) increase in the mean body size of marine turtles from the Jurassic to the Early Cretaceous, and a small drop in the Late Cretaceous (Figure 4 c, d), but the latter shows the highest variability body sizes among marine turtles in the series (Figure 4c). After the K-Pg transition, the range of body sizes decreases substantially in the marine group, but the mean remains similar. After that, a significant increase in mean body size (p-value = 0.003958; Table 3), from 41.3 to 103.6 cm was detected from the Neogene to the Quaternary (Figure 4c, d).

Patterns by taxonomic group

Patterns of body size evolution differ considerably between taxonomic groups (Figure 5). Most groups seem to have maintained a constant body size disparity throughout their evolution, such as most stem-turtles (Figure 5a). Americhelydia and Testudinoidea show a wide range of body size early in their evolutionary history (Figure 5e, f). Non-Kinosternidae Americhelydia exhibit considerably large body sizes, whereas the diversification of Kinosternidae after the K-Pg boundary increases the body size range of americhelydians (Figure 5e). Similarly, Testudinoidea reached its maximum disparity in the Neogene, after the divergence of the crown-groups (Figure 5f). Within Trionychia, the extinct Adocusia reached larger body sizes before the K-Pg boundary, whereas the range of body sizes within Trionychidae, which includes most trionychian species, expanded only after that boundary. Other groups appear to show different trends. Meiolaniformes and Pan-Podocnemididae (Figure 5a, b) exhibit an apparent trend of increasing body size through time. Meiolaniformes attained larger maximum body sizes than any other member of the stem lineages to Testudines (Figure 5a), but the earlier taxa were comparatively smaller. Bothremydids seem to have expanded their range of body sizes until their extinction in the Paleogene, whereas other pan-podocnemidids appear to have shifted their size distributions towards larger MCLs throughout their evolutionary history (Figure 5b). Interestingly, the only group that shows an apparent decrease in body size through time is another pleurodiran lineage, Chelidae (Figure 5d). The first pan-chelids were medium-sized, but by the Late Cretaceous they attained their largest sizes. Extant chelids, however, display smaller body sizes than their extinct representatives and stem-Pleurodira.

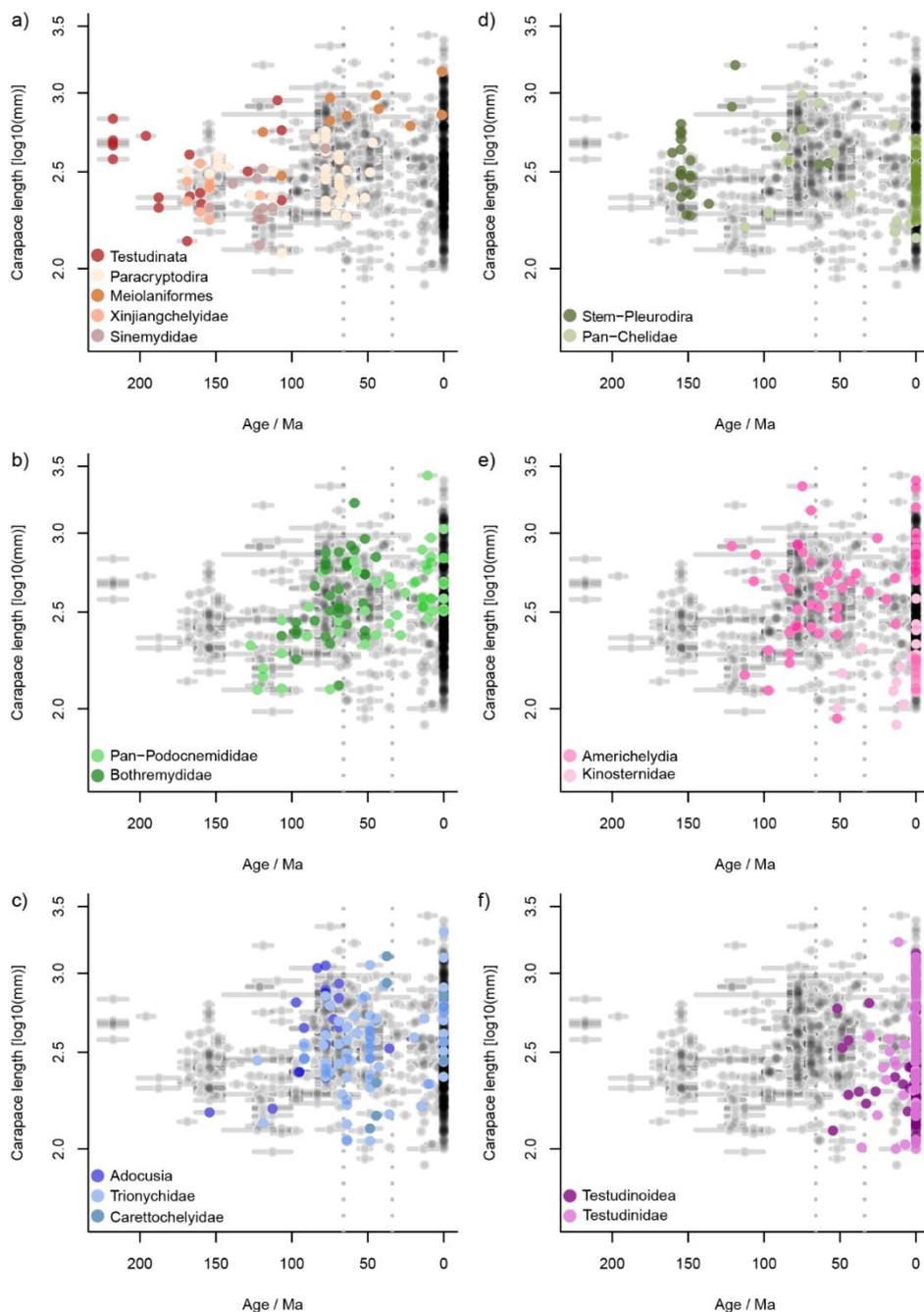


Figure 5. Body sizes of different taxonomic turtle groups (colored circles) — based on the “Ev19” topology — across the K- Pg and Eocene-Oligocene boundaries (vertical gray dot line). Testudinata are represented in (a) by non-testudines testudinates, not including the other groups represented in this figure. In (b), Pan-Podocnemididae does not include Pelomedusidae and Bothremydidae. In (e), Americhelydia designates all Americhelydia non-kinosternids. In (f), Testudinoidea designates all Testudinoidea non-testudinids.

Ancestral state reconstructions

Ancestral state reconstructions based either on the “Ev19” (Figure 6a, b) or the “St18” supertrees show similar results (Figure 6c, d). For this reason, the description below is based solely on the “Ev19” supertree, but highlighting significant differences to the results of “St18” when those exist.

When the fossil taxa are included in the reconstructions, the ancestral size estimates for most of the more diverse groups (e.g., Testudines, Pleurodira, Pelomedusidae, Chelidae, Cryptodira, Trionychia, Testudinoidea, and Americhelydia) was similar, with MCL values below 50 and above 25 cm (Figure 6a). Among the stem-turtles, Paracryptodira and Meiolaniformes have similar ancestral values, but whereas paracryptodires float around this ancestral value, meiolaniids increase their sizes along time (see section “Patterns by taxonomic group”). Among pleurodires, several branches that split before the origin of Podocnemididae show smaller sizes (between 10 and 25 cm), but the ancestral to all podocnemidids was likely a larger turtle (between 30 and 50 cm). Within Cryptodira, the crown-groups Testudinidae, Geoemydidae, and Emydidae had smaller estimated ancestral sizes (between 10 and 25 cm) in relation to their Testudinoidea ancestor (between 25 and 30 cm; Figure 6a). The Americhelydia node (30-50 cm), on the other hand, shows an intermediate value between Chelonioidae (> 50 cm) and Kinosternoidea (< 30 cm). Noteworthy, Kinosternidae was one of the few main clades with an estimated ancestral size below 20 cm.

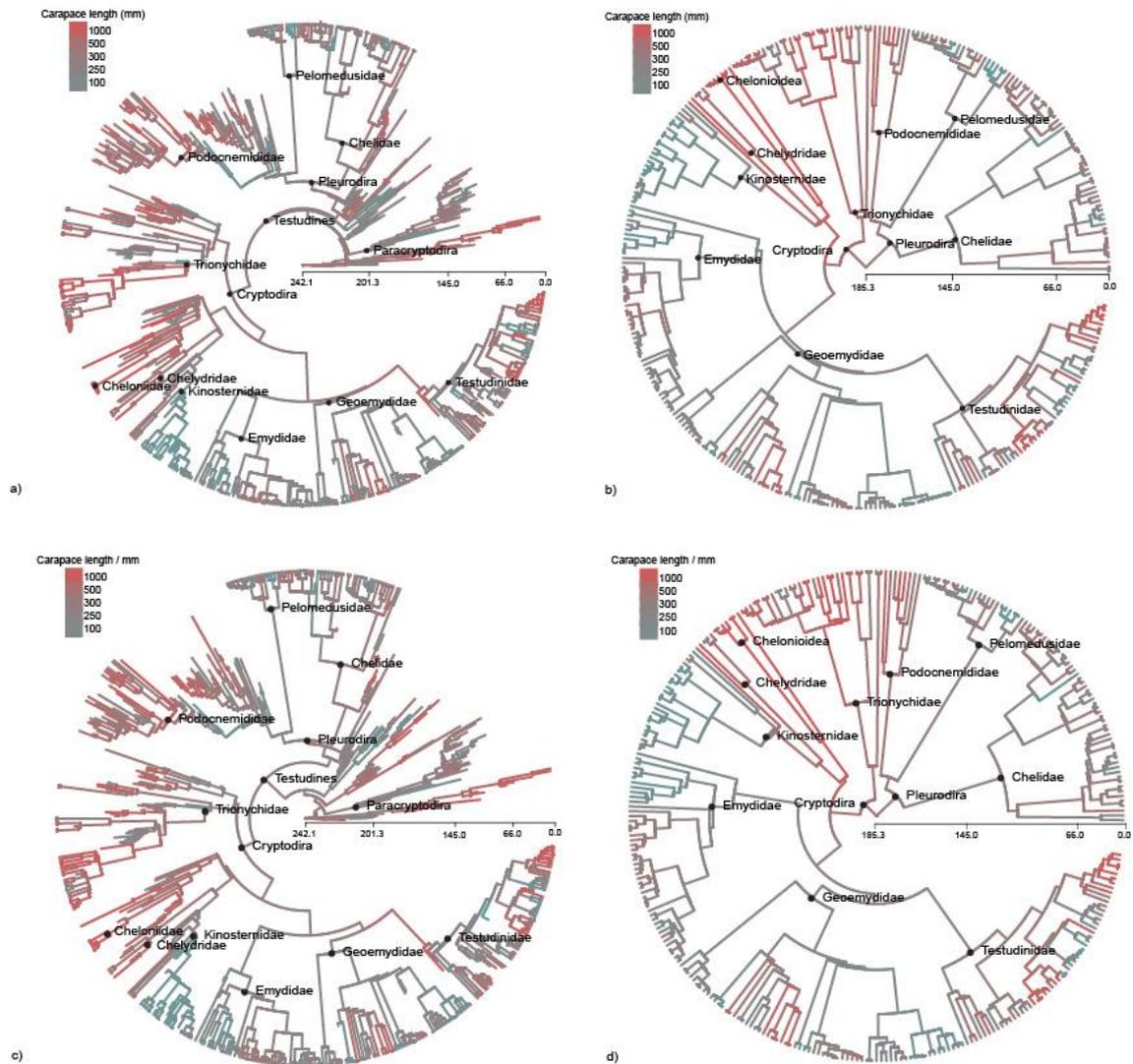


Figure 6. Ancestral state estimates (= ancestral body sizes), using the “Ev19” (a and b) and the “St18” (c and d) supertree topologies, of body sizes using: (a) and (c) the complete tree, including fossils; and (b) and (d): an extant-only subtree, excluding all fossils. Large body sizes are represented by pink shades, while small body sizes are represented by blue gray shades.

The inclusion of fossils changed the ancestral body size reconstructions of most main lineages (Figures 6 and 7). Nonetheless, no specific trend is noted when paleontological data is included and the magnitude of the differences also varied greatly. For some groups (e.g., Chelidae, Podocnemididae, Emydidae, and Geoemydidae), the inclusion of extinct taxa increased the estimated body sizes, whereas for others (e.g., Pelomedusidae, Trionychidae, Testudinidae, Chelydridae, Kinosternidae, and Cheloniidae) a decrease in the estimates was observed. The most significant changes were seen in Cryptodira,

Trionychidae, Chelydridae, Kinosternidae, and Cheloniidae. It is worth noting that, compared to previous studies, even a small difference in fossil sampling changed the estimates. For instance, the ancestral body size for Pan-Testudinidae — based on 78 taxa (25 extinct taxa and 53 living ones) — is larger than that of Vlachos & Rabi (2018), which included 59 taxa (36 extinct and 23 living species).

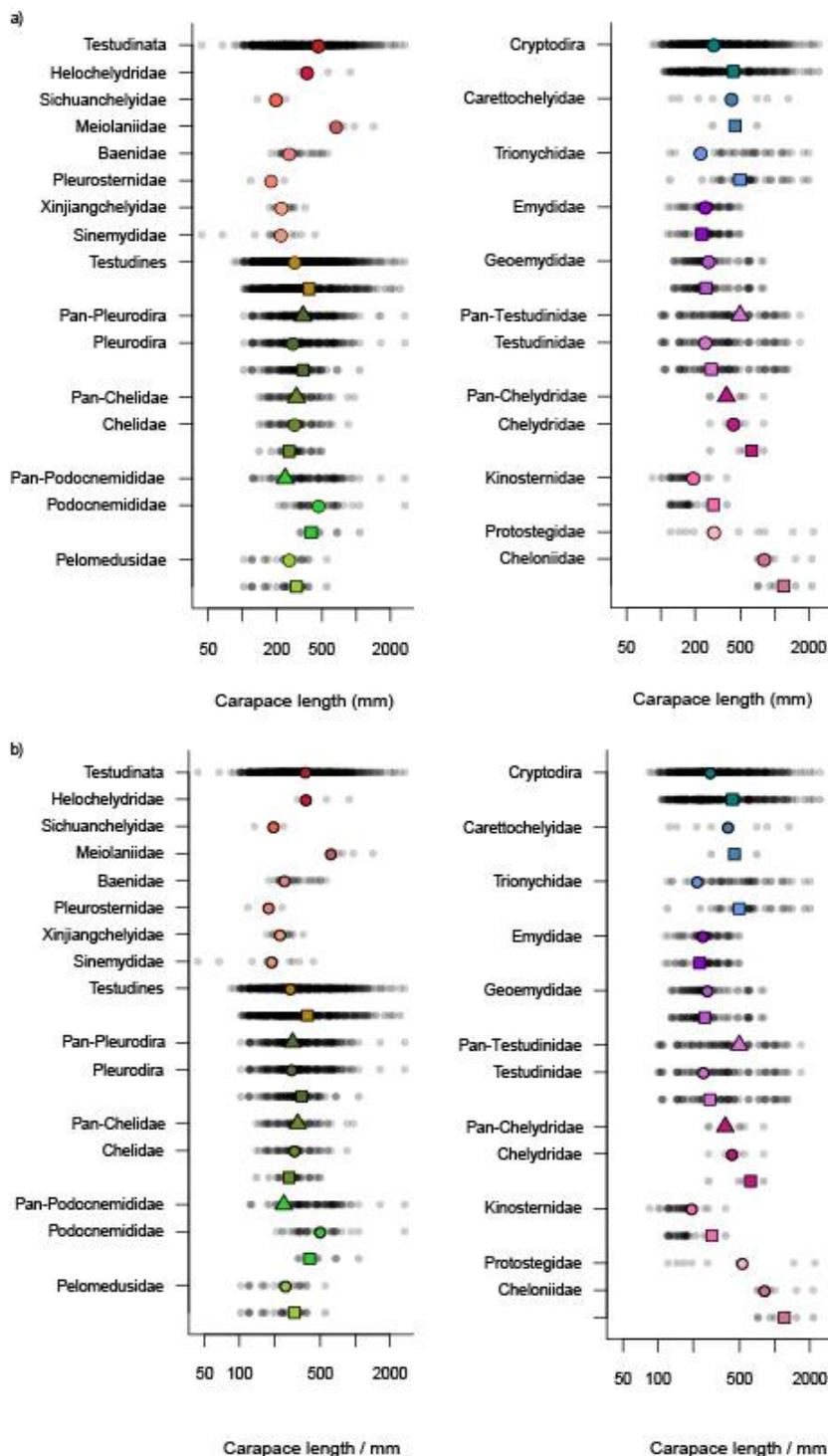


Figure 7. Ancestral body sizes estimated for different taxonomic turtle groups. a) using the “Ev19” supertree topology, and b) using the “St18” supertree topology. Small grey dots indicate all taxa within that lineage. Colored triangles represent the ancestral estimates of stem-groups; circles represent ancestral estimates of the crown-groups and squares represent ancestral estimates of the crown-groups without the fossil taxa.

Body size vs. paleotemperature

No correlation was observed between global paleotemperature and mean body size of Testudinata or Cryptodira through time (Table 4; Figure 8). On the contrary, pleurodiran turtles showed a weak, but significant correlation (OLS: p-value = 0.0477; $R^2 = 0.1561$). Yet, this was found only when using the Zachos et al. (2008) temperature dataset (from Maastrichtian to Quaternary) and with the time bins divided by chronostratigraphic Stages. All other correlation tests for Pleurodira (i.e., using the Zachos et al. [2008] dataset or equal time bins of 10 or 5 Ma) were not significant.

I also analyzed body size disparity through time (using the standard deviation of body sizes as a disparity metric) and found opposite results (Table 5; Figure 9): significant correlations were found for the datasets with all Testudinada and only with cryptodirans. Using the Prokoph et al. (2008) dataset, significant correlations with testudinates body size disparity was found using all time bins schemes: 10 Ma: p-value = 0.008 (GLS), p-value = 0.0221 (OLS); 5 Ma: p-value = 0.0383 (GLS), p-value = 0.005877 (OLS); Chronostratigraphic Stages: p-value = 0.0008 (GLS), p-value = 0.00001 (OLS). For the Cryptodira dataset, significant correlation was found using Zachos et al (2008) dataset and the time bins divided by chronostratigraphic Stages: (GLS: p-value = 0.04; OLS: p-value = 0.07). For the dataset including only pleurodirans, however, no significant correlation was found.

Table 4. Results of correlations tests (GLS and OLS) between paleotemperature and mean body size — using 10 Ma time bins, 5 Ma time bins, and chronostratigraphic stages. The tests were performed using data from the Triassic to Recent, but also from the Maastrichtian to Recent. Tests were performed using all available turtles in the dataset, as well as only pleurodirans and only cryptodirans.

All turtles								
	GLS				OLS			
	Phi	Intercept	Slope	AIC	R²	Intercept	Slope	AIC
10 Ma time bins – Triassic	0.7810034	2.5023858	-0.0209698 (p-value= 0.2603)	-47.6995	0.1161	2.4468891	-0.0493167 (p-value= 0.0721)	-32.52513
10 Ma time bins – Maastrichtian	0.06457515	2.570258	-0.009850 (p- value=0.434)	-24.06881	-0.02369	2.571342	-0.010446 (p-value= 0.396)	-26.04175
5 Ma time bins – Triassic	0.8456039	2.5156845	-0.0054801 (p-value= 0.7101)	-94.11317	0.01618	2.4666230	-0.0266091 (p-value= 0.218)	-55.13755
5 Ma time bins – Maastrichtian	0.2923064	2.5547706	-0.0030103 (p-value= 0.7793)	-52.30159	-0.07245	2.5551354	-0.0030148 (p-value= 0.7332)	-53.06143
Stage time bins - Triassic	0.8326693	2.5171651	-0.0073077 (p-value= 0.5624)	-118.0351	-0.000824	2.4878601	-0.0176867 (p-value= 0.3314)	-76.72058
Stages time bins – Maastrichtian	0.3667753	2.5254906	0.0231871 (p- value=0.3921)	-37.50605	0.03343	2.5207556	0.0257438 (p-value= 0.1893)	-35.86134
Pleurodira								
	GLS				OLS			
	Phi	Intercept	Slope	AIC	R²	Intercept	Slope	AIC
10 Ma time bins - Maastrichtian	-0.1104746	2.6890773	-0.0433811 (p-value= 0.1214)	-13.12209	0.3076	2.6945414	-0.0471775 (p-value= 0.1137)	-15.07229
5 Ma time bins - Maastrichtian	0.1833449	2.667117	-0.026230 (p- value=0.3038)	-26.06354	-0.001091	2.6615226	-0.0211943 (p-value= 0.3404)	-27.7351
Stages time bins - Maastrichtian	0.5782211	2.6971864	-0.0397538 (p-value= 0.1296)	-49.4855	0.1561	2.6967131	-0.0343025 (p-value= 0.0477)	-44.78507
Cryptodira								
	GLS				OLS			
	Phi	Intercept	Slope	AIC	R²	Intercept	Slope	AIC
10 Ma time bins - Maastrichtian	-0.299118	2.5377580	-0.0230125 (p-value= 0.3622)	-11.99757	-0.16	2.5208534	-0.0113347 (p-value= 0.6951)	-13.64388
5 Ma time bins - Maastrichtian	0.07835617	2.4988045	-0.0137193 (p-value= 0.512)	-28.84233	-0.02506	2.5012943	-0.0158128 (p-value= 0.425)	-30.78183

Stages time bins - Maastrichtian	0.6081662	2.4725167	0.0138192 (p-value=0.7366)	-31.20058	-0.03396	2.4702452	0.0117112 (p-value=0.6498)	-21.31404
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Table 5. Results of correlations tests (GLS and OLS) between paleotemperature and standard deviation of body sizes — using 10 Ma time bins, 5 Ma time bins, and chronostratigraphic stages. The tests were performed using data from the Triassic to Recent, but also from the Maastrichtian to Recent. Tests were performed using all available turtles in the dataset, as well as only pleurodirans and only cryptodirans.

All turtles								
	GLS				OLS			
	Phi	Intercept	Slope	AIC	R²	Intercept	Slope	AIC
10 Ma time bins- Triassic	0.693654	0.271527	0.044182 (p-value=0.008)	-57.012	0.2067	0.277518	0.047309 (p-value=0.0221)	-45.5699
10 Ma time bins - Maastrichtian	-0.4259	0.253754	0.007586 (p-value=0.35)	-27.0085	-0.1017	0.255554	0.006813 (p-value=0.5337)	-27.4254
5 Ma time bins – Triassic	0.782084	0.254962	0.026655 (p-value=0.0383)	-107.702	0.1792	0.282543	0.044639 (p-value=0.0059)	-79.1472
5 Ma time bins – Maastrichtian	0.218869	0.25124	0.013277 (p-value=0.124)	-58.0527	0.2193	0.249185	0.014849 (p-value=0.052)	-59.4153
Stage time bins – Triassic	0.786753	0.28017	0.033001 (p-value=0.0008)	-146.314	0.4036	0.313497	0.057868 (p-value=0.00001)	-115.606
Stage time bins - Maastrichtian	0.196118	0.265409	0.001501 (p-value=0.8794)	-76.7083	-0.04171	0.26526	0.001628 (p-value=0.8452)	-77.6993
Pleurodira								
	GLS				OLS			
	Phi	Intercept	Slope	AIC	R²	Intercept	Slope	AIC
10 Ma time bins - Maastrichtian	0.145399	0.231859	-0.0131 (p-value=0.4921)	-18.6701	-0.08878	0.228715	-0.01193 (p-value=0.5068)	-20.5307
5 Ma time bins - Maastrichtian	0.412774	0.21046	-0.00386 (p-value=0.8131)	-43.6373	0.08035	0.200686	0.002237 (p-value=0.8587)	-43.176
Stage time bins - Maastrichtian	0.668839	0.23174	-0.00912 (p-value=0.8587)	-69.2207	0.04721	0.200686	0.002237 (p-value=0.7092)	-43.176
Cryptodira								
	GLS				OLS			
	Phi	Intercept	Slope	AIC	R²	Intercept	Slope	AIC
10 Ma time bins - Maastrichtian	-0.4319	0.269509	0.002648 (p-value=0.7813)	-24.0946	-0.1453	0.265835	0.005976 (p-value=0.6456)	-24.8887
5 Ma time bins - Maastrichtian	0.075838	0.253553	0.013336 (p-value=0.1422)	-53.1929	0.1182	0.253464	0.013299 (p-value=0.1236)	-55.1134
Stage time bins - Maastrichtian	-0.08545	0.290948	-0.0167 (p-value=0.0459)	-73.9715	0.1007	0.290544	-0.01644 (p-value=0.06732)	-75.7955

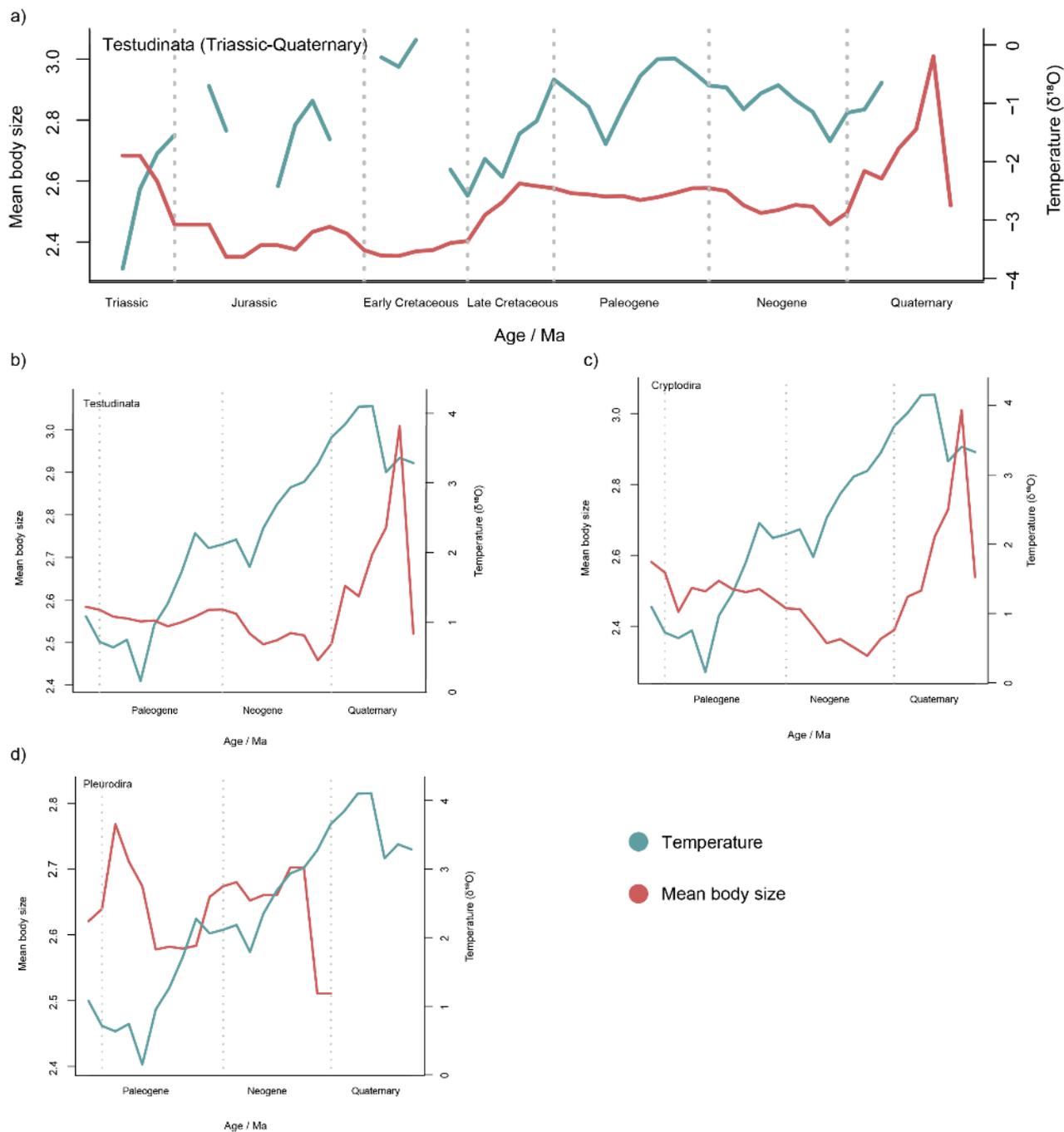


Figure 8. Paleotemperature and mean body size curves through time. a) Testudinata curve from the Triassic to Recent. b) Testudinata curve from de Maastrichtian to Recent; c) Cryptodira curve from de Maastrichtian to Recent b) Pleurodira curve from de Maastrichtian to Recent. I used paleotemperature dataset available in Prokoph et al. (2008) in (a), and Zachos et al. (2008) in (b-c).

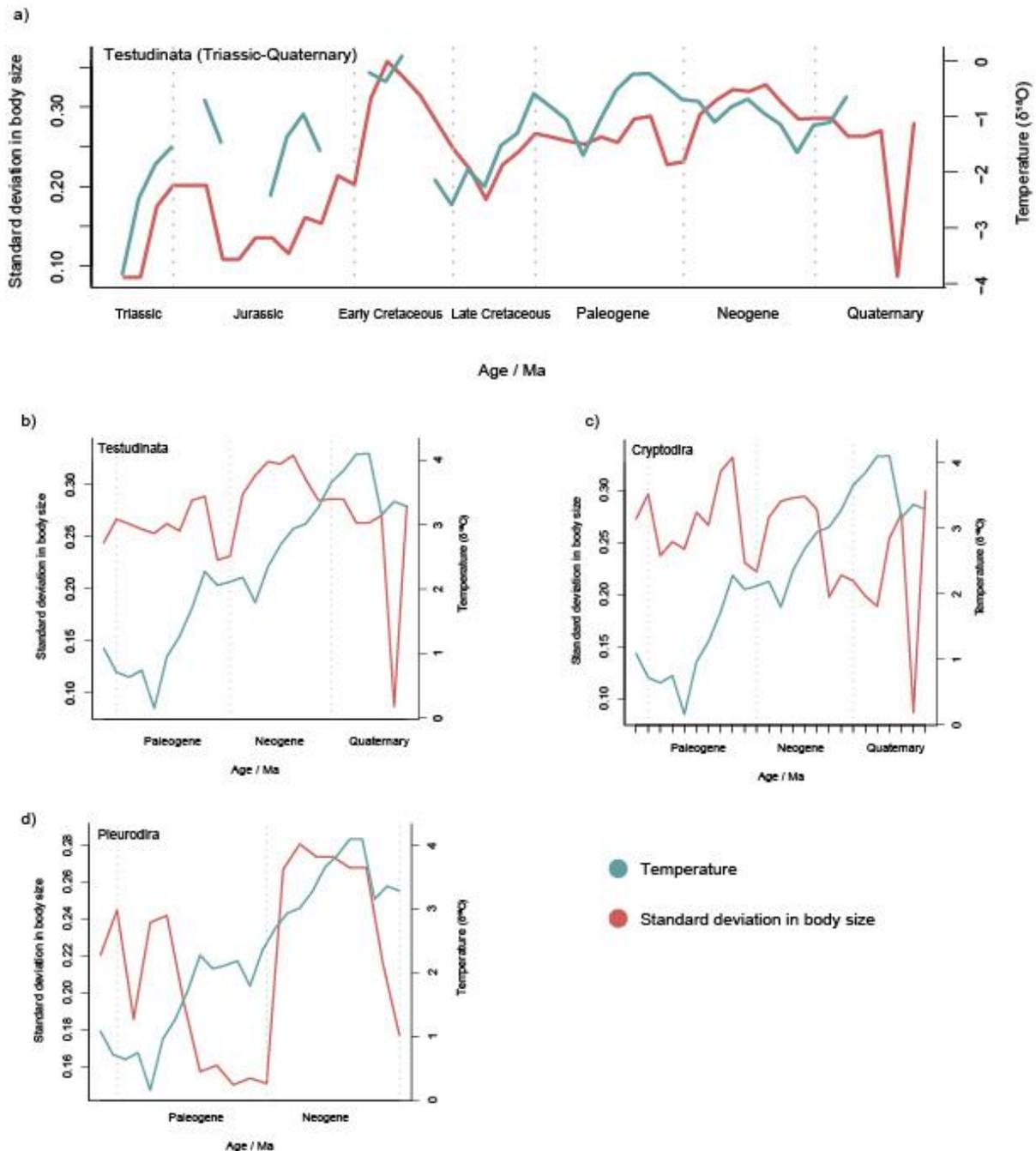


Figure 9. Paleotemperature and standard deviation in body size curves through time. a) Testudinata curve from the Triassic to Recent. b) Testudinata curve from de Maastrichtian to Recent; c) Cryptodira curve from de Maastrichtian to Recent b) Pleurodira curve from de Maastrichtian to Recent. I used paleotemperature dataset available in Prokoph et al. (2006) in (a), and Zachos et al. (2008) in (b-c).

Model fitting

The AICc scores for all the evolutionary models fitted to the turtle body size data and trees show an overwhelmingly stronger support (i.e., lower AICc values) for the uniform

OU model, even when compared to the non-uniform multi-trend models. Consistently, this stronger support for the OU model was found when using either the “Ev19” or the “St18” topologies (Figure 10). These results rule out the presence of trend-like processes (either uniform or multi-trend) in the body size evolution of Testudinata, at least when the entire tree is considered.

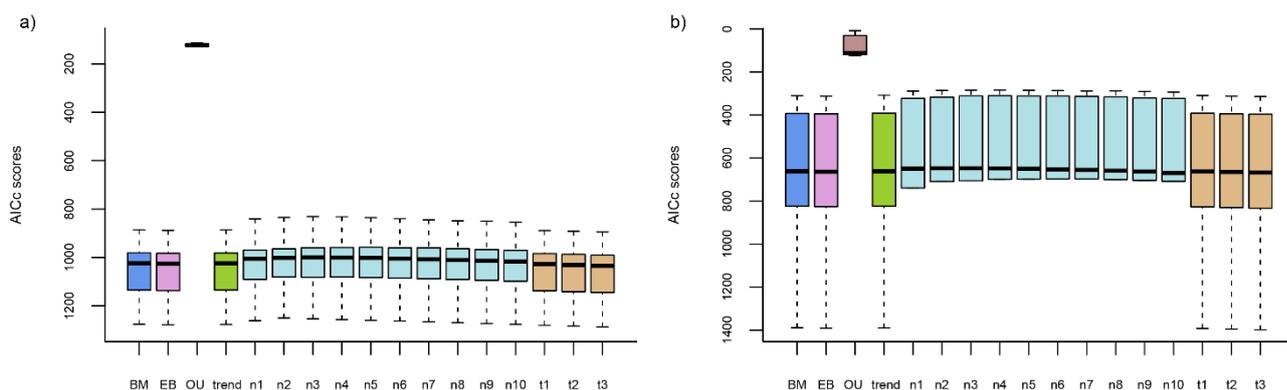


Figure 10. AICc scores for all evolutionary models fitted to a) “Ev19” supertree, and b) “St18” supertree. “n” and “t” stand for “node shift model” and “time shift model”, respectively. Lower AICc scores indicate higher support.

Discussion

The influence of fossils on body size patterns and ancestral estimates

Despite past controversies (e.g., Patterson, 1981), it has become increasingly clear that the paleontological record is crucial to answer macroevolutionary questions (Quental & Marshall, 2010; Louca & Pennell, 2020). It is particularly evident the influence that fossils have on the results of ancestral state estimates and on evolutionary rates of trait evolution (e.g., Slater et al., 2012; Puttick, 2016). Nevertheless, extinct taxa are rarely explicitly included in such analyses (Angielczyk et al., 2015): in macro-analyses of turtle body size, a single publication has done so (Vlachos & Rabi, 2018). As noted by Jaffe et al. (2011), examining the evolution of body size in the fossil record of turtles might provide new insights not revealed by previous analyses.

Based on a sample of 536 extinct taxa, this study is the first comprehensive attempt in this direction and I confirm its impact on both the estimates of divergence times (Figure 1 and 2; Appendix 4) and of ancestral body sizes (Figures 6 and 7). The age estimates for older nodes (Testudines, Cryptodira, and Pleurodira) are consistently younger when fossils are considered (Figure 11; see also Sterli et al., 2018). For younger divergences (Durocryptodira, Americhelydia, Testudinoidea, and Pelomedusoides), the estimates are older in comparison to molecular studies, except for Trionychia and Chelidae, in which two molecular studies retrieved older ages (Trionychia: Joyce et al., 2013 & Thomson et al., 2021; Chelidae: Joyce et al., 2013 & Pereira et al., 2017). Both clades have a long (Trionychia = 18 Ma; Chelidae = 43 Ma) ghost lineage towards their crown-group. It is noteworthy that the only other previous analysis including fossils as tips and using the FDB method for estimating divergence times for turtles (i.e., Sterli et al., 2018) provided earlier ages in all sampled nodes, as well as less uncertainty (Figure 12). Although Sterli et al. (2018) performed total-evidence analyses, that simultaneously infer tree topology and divergence times (which is not the case here), the most striking difference between the two studies is the sampling; Sterli et al. (2018)'s matrix included only 99 taxa (30 extant and 69 fossils). Thus, the results show that, in comparison to molecular analyses, the inclusion of fossils tends to provide earlier estimates for older nodes and later ages for younger ones. In previous studies including fossils, better sampling usually provides younger, but more uncertain ages (Luo et al., 2020).

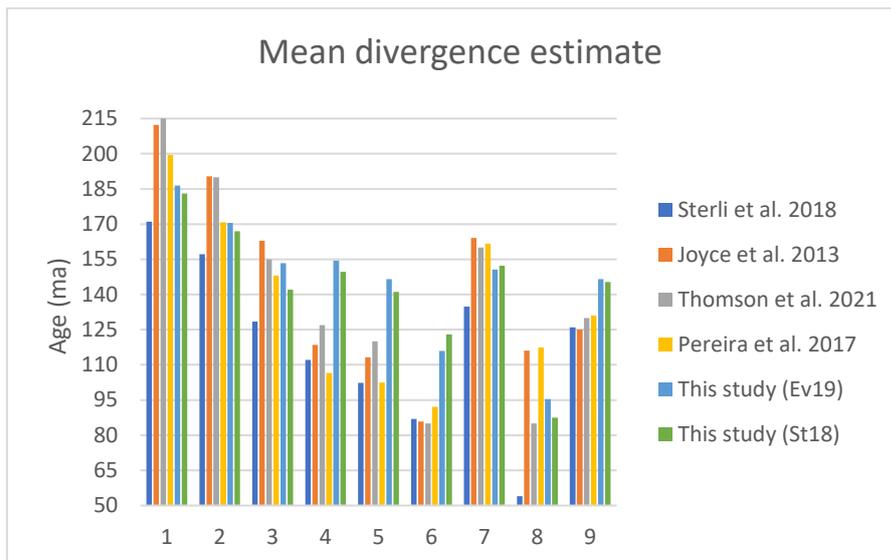


Figure 11. Median age comparison between the topologies and previous studies. Numbers in the x-axis represent different clades: 1: Testudines; 2: Cryptodira; 3: Trionychia; 4: Durocryptodira; 5: Americhelydia; 6: Testudinoidea; 7: Pleurodira; 8: Chelidae; and 9: Pelomedusoides.

Estimates of ancestral body sizes were affected by the inclusion of fossils in most lineages assessed here, but to different degrees (Figure 6). In other words, there seems to be no predictable effect on the reconstructions. For example, both Podocnemididae and Chelidae had increased ancestral sizes when fossils were considered (Figure 6), but younger podocnemidid taxa are larger than the older ones, whereas the opposite is the case for chelids (Figure 7). Likewise, two lineages with a poor fossil records, Geoemydidae and Kinosternidae, which show no apparent difference in size between extinct and extant taxa (Figure 6), display inverse effects on ancestral estimates: fossils increase ancestral body size in geoemydids, but decrease in kinosternids (Figure 7). In summary, although no clear pattern is observed here, we understand the inclusion of fossils in these analyzes as important for a more accurate estimate of the history of the lineages (Finarelli & Flynn, 2006).

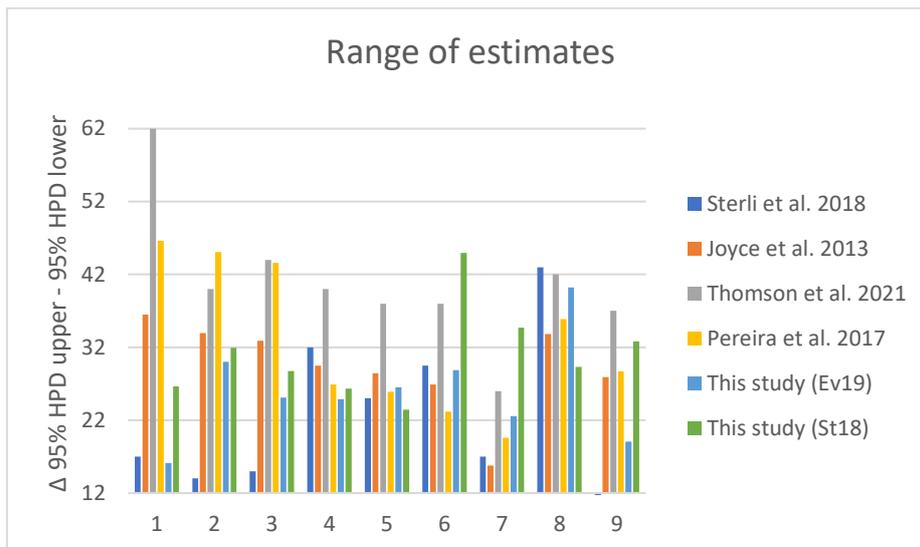


Figure 12. Variation in highest posterior density (HPD) age ranges comparison between the topologies and previous studies. Numbers in the x-axis represent different clades: 1: Testudines; 2: Cryptodira; 3: Trionychia; 4: Durocryptodira; 5: Americhelydia; 6: Testudinoidea; 7: Pleurodira; 8: Chelidae; and 9: Pelomedusoides.

Body size evolution and ecological habitats

Since the Jurassic, most turtles are freshwater (Figure 4b; Joyce & Gauthier, 2004). That ecological group had a fairly homogeneous body size disparity (=range of body sizes) through time, which is the highest among turtles for most of their geological history. Exceptions are the Late Cretaceous and the Quaternary, when marine and terrestrial turtles, respectively, exceed the range of body sizes seen in their freshwater relatives (Figure 4d). The wide and constant range of body sizes of freshwater turtles might be explained by distinct evolutionary scenarios within such environments (Jaffe et al., 2011). Different species from closely or far related lineages inhabit several disparate freshwater environments (Bonin et al., 2006). Some taxa acquired, for instance, resistance to estuarine or brackish water in different pleurodiran or cryptodiran lineages (Bower et al., 2016; Agha et al., 2018). Also, closely related taxa occupying the same areas are known to avoid competition through body size divergence, such as extant podocnemidids (Cunha et al. 2020) and trionychids (Pritchard, 2001).

Terrestrial and marine turtles, on the other hand, represent fewer lineages, with less constant evolutionary histories. The earliest turtles were terrestrial and all showed medium to large sizes during the Mesozoic (Figure 4a, d). Meiolaniformes is the only of these stem-lineages to survive until fairly recently (Sterli, 2015) and after the Mesozoic they are all large to gigantic, with a potential trend towards size increase (Figure 5a; see also section “Cope’s rule and trends of body size evolution”). Pan-testudinids — the only extant lineage of terrestrial turtles — appear in the fossil record during the Paleogene and remain relatively small at least until the Eocene-Oligocene transition (Figure 5f). This period (Eocene-Oligocene) is congruent with a peak of diversification related to the origin of crown-Testudinidae and Testudona (Lourenço et al., 2012; Vlachos & Rabi, 2018), after which the group spread from Eurasia to most of the world. Therefore, the recent high variation in body size within tortoises might be also related to the expansion of occupied habitats (similar to freshwater turtles). Additionally, larger sizes in insular species are thought to be associated with the ability of marine dispersal, and could have been maintained due to the higher endurance required to stand variable climatic conditions and periods of scarce resources (Meylan & Sterrer, 2000; Jaffe et al., 2011; Vlachos & Rabi, 2018). Similarly, marine dispersal has been suggested as an explanation for the large size of Cenozoic Meiolaniformes (Figure 5a; Sterli, 2015), which is in agreement with Jaffe et al. (2011) hypothesis of gigantism in terrestrial turtles.

On the contrary, extant marine turtles exhibit low disparity, but impressively large body sizes (Figure 4c), which has been suggested to be associated with various reasons, including thermoregulation (Mrosovsky, 1980) and high dispersal abilities required for migration in the group (Jaffe et al., 2011). A similar pattern of larger sizes in marine species have been reported for crocodylomorphs, which has been explained by physiological constraints associated with thermoregulation and lung capacity (Godoy et

al., 2019; Gearty & Payne, 2020). However, the fossil record of marine turtles also shows that they also occupied other regions of the body size spectrum in the past (Figure 4c, d), e.g., *Santanachelys gaffneyi* from the Early Cretaceous of Brazil, is one of the oldest and smallest sea turtles (20 cm; Hirayama, 1998).

Chelonioidea, the extant group of sea turtles, presents a morphology highly adapted to the marine environment, including limbs modified into paddles and reduced shell ossification, which allows them to explore pelagic environments (Bardet et al., 2014; Evers & Benson, 2019). Regardless of the uncertain phylogenetic affinities of Thalassocheilydia (Eurysternidae, Plesiochelyidae, and Thalassemydidae) among other sea turtles (Anquetin et al., 2017; Evers & Benson, 2019), they were probably not as well-adapted to marine habitats as chelonioids, likely indicating a more shallow, coastal, and brackish habitat preference (even though fully marine in some lineages; Anquetin et al., 2017; Eves & Benson, 2019). Likewise, the pleurodiran marine turtles — Bothremydidae — are usually described as near-shore species (Gaffney et al., 2006; Ferreira et al., 2018). Both these clades have higher body size disparities and are not strongly associated with larger sizes (Figures 4, 5). Thus, larger body sizes in sea turtles might indeed be related to the origin of a pelagic lifestyle and adaptations to this habitat.

Bergmann's rule and temperature

The relationship between abiotic factors and body size has been extensively studied, and different vertebrate groups seem to be differently affected, especially when it comes to comparing endothermic and ectothermic organisms (van Voorhies, 1996; Partridge & Coyne, 1997; van der Have & de Jong, 1996; Mousseau, 1997; Angilletta et al., 2004; Ashton & Feldman, 2003; Angielczyk et al., 2015). Specifically, large-scale trends such as the Bergmann's rule (i.e., the tendency of having larger sizes at higher latitudes) seem

to play an important role for endotherms (James, 1970; Zink & Remsen, 1986; Ashton et al. 2000), but results for ectothermic reptiles are more controversial (Mousseau, 1997; Ashton & Feldman, 2003).

In turtles, the potential influence of Bergmann's has been investigated previously. Angielczyk et al. (2015) did not find support for Bergmann's rule, contradicting a previous study (Ashton & Feldman, 2003). Instead, they found the opposite: large body sizes tend to be more common at lower latitudes, whereas small body sizes occur more frequently at higher latitudes (Angielczyk et al., 2015). The explanation proposed by the authors for the inversed pattern is that the warmer climates of lower latitudes would enable further growth during the life span of the individuals (Angielczyk et al., 2015). This pattern, which is consistent with what is proposed for ectothermic organisms (Makarieva et al., 2005; Head et al., 2009; Angielczyk et al., 2015), has been suggested as an explanation for the large body size of several turtle species, such as *Stupendemys geographicus* — a giant pleurodiran with 2.4 m of carapace length from Miocene of South America — and the giant soft-shell turtles of North America during the warmer conditions of 70-46 million years ago (Vitek, 2012; Cadena et al., 2020).

Even though I did not explicitly test for a correlation between body size and paleolatitude, I could evaluate the explanation proposed by Angielczyk et al. (2015) by testing its relationship with paleotemperature. In general, the results do not support a relationship between larger body sizes and higher temperatures (Table 4). Both long- (Figure 8a) and short-term curves (Figure 8b–d) of mean body size through time do not seem to follow the same pattern of paleotemperature variation. A possible exception was the Pleurodira mean body size, which shows a weak, but significant correlation with the Cenozoic (Zachos et al., 2008) paleotemperature variation (Table 4; Figure 8c). Interestingly, Podocnemididae and Chelidae plots of body size through time (Figure 5b,

d) were the only ones (in addition to maybe Meiolaniformes; Figure 5a) to show an apparent trend of body size change towards opposite body sizes (higher for Podocnemididae and lower for Chelidae). Angielczyk et al. (2015) found a positive correlation between latitude and body size in Chelidae (Pleurodira) and the lower temperatures after the Cenomanian was proposed to have affected the distribution of Chelidae (Ferreira et al., 2018).

When Testudinata body size disparity (=standard deviation) through time is plotted with paleotemperature, however, periods of higher disparity are observed when temperatures are also higher, and low disparity are seen in periods of lower temperatures (Figure 9a; Table 5). Periods of high temperature allows turtles occupy different niches in higher latitudes and, consequently, acquire greater morphological disparity (Cleary et al., 2020).

At the same time, Vlachos & Rabi (2018) also did not find correlations between environmental temperature and body size, and the authors proposed that gigantism occurred multiple times within Pan-Testudinidae. Temperature has been a commonly proposed explanation for body size variation in different species and clades of turtles, and it may have some effect — in terms of disparity, diversity, or distribution — in particular lineages (e.g., Böhme, 2003; Vitek, 2012; Georgalis & Kear, 2013; Ferreira et al., 2018).

Cope's rule and trends of body size evolution

Cope's rule is another large-scale trend of body size evolution that has been heavily debated, but remains controversial (Hone & Benton, 2005). Positive results seem to receive good support from analyses using fossil data (although with many exceptions), but not so much when the focus is on extant taxa (Moen, 2006). Only Moen (2006) investigated the effect of Cope's rule in the evolution of body size in turtles, but found no

support for it. The author has limited the analysis to extant cryptodires and suggested that further studies accounting for the paleontological data might provide further insights. Here, even though I employed a large dataset including both the extant and extinct diversity of turtles, I also found no support for a trend-like process towards body sizes in turtles (Figure 10), which would best represent the Cope's rule. Therefore, I demonstrate that the Cope's rule cannot offer a general explanation for the evolution of larger body sizes in Testudinata. This is true when the entire tree of Testudinata is considered. Nevertheless, I did not apply model fitting analyses to specific lineages — e.g., Cryptodira and Pleurodira —, which could still provide evidence for a trend-like mode of evolution.

Conclusions

1. A new time-calibrated supertree, including 846 extinct and living turtle species, is provided, in addition to a comprehensive dataset of carapace lengths, chronostratigraphic and habitat data for 795 taxa. Together, these data should help improving the breadth of macroevolutionary studies in the group.
2. Even though there are differences between ancestral state reconstruction performed with and without the fossil taxa, the effect of this inclusion varies across the lineages.
3. Through time distributions of body sizes show that Testudinata reached substantial disparity (=range in body sizes) only in the Early Cretaceous, concomitantly with the lowest mean body size in their evolutionary history. Body size was not significantly affected during the K-Pg, and, after that, disparity and mean body sizes remains fairly constant.
4. Freshwater turtles show a constant range of body sizes and higher disparity through time, which might be related to the ecological diversity of the habitats these turtles inhabit. Body size in terrestrial turtles is explained by their ecological diversity, in addition to the higher dispersal ability in giant species. In sea turtles,

adaptations to pelagic lifestyle are likely related to their larger body sizes, especially in the Quaternary.

5. No support for Cope's rule was found, meaning that the larger sizes obtained by some turtles was not achieved by a general trend-like process.
6. Only very weak or not significant correlation was found between mean turtle body size and paleotemperature, indicating that a trend such as the Bergmann's rule has no support for the group.
7. A significant correlation was found between paleotemperature and body size disparity (=standard deviation) for Testudinata and Cryptodira, suggesting that higher temperatures favor body variation in the group, possibly by allowing the occupation of more habitats and niches.

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Appendices

Appendix 1 - Supplementary references

TESTUDINATA: Evers, Barret, & Benson (2019); Sterli, de la Fuente, & Rougier (2018).

*Joyce (2017): used to include taxa that were not sampled by the above topologies.

-MEIOLANIFORMES: Sterli, de la Fuente, & Krause (2015); Sterli, de la Fuente, & Rougier (2018).

*In Ev19: the position of *Chubutemys* and *Kallokibotion* were defined according to Evers, Barret, & Benson (2019).

-HELOCHELYDRIDAE: Joyce (2017).

**Aragochersis*: according to Pérez-García, Espílez, Mampel, & Alcalá (2019).

-SICHUANCHELYIDAE: Joyce (2017).

-COMPSEMYDIDAE: Joyce & Anquetin (2019).

**Peltochelys duchastelii*: according to Joyce & Rollot (2020).

-PARACRYPTODIRA: Joyce & Rollot (2020).

* position of *Dinochelys*, *Compsemydidae*, *Uluops* e Baenoidea.

-BAENIDAE: Joyce & Lyson (2015).

*Eubaeninae (Lyson, Sayler, & Joyce, 2019) + “Baena” escavada (Joyce & Lyson 2015).

-PLEUROSTERNIDAE: Joyce & Rollot (2020).

Siamochelys peninsularis: according to Sterli, de la Fuente, & Rougier (2018).

*sister group of Paracryptodira

-XINJIANGCHELYIDAE: Pérez-García, Gasulla, Ortega (2014); *Xinjianchelys* (less inclusive clade) according to Evers, Barret, & Benson (2019).

Sampled made by Evers & Benson (2019) and Evers, Barret, & Benson (2019) include:

Xinjianchelys radiplicatooides, *Xinjianchelys wusu*, *Annemys* IVPP V18106, *Annemys levensis*, and *Annemys latiensi*. *A. latiensi* and *A. levensis* are included in Pérez-García,

Gasulla, Ortega (2014) as *Xinjianchelys latiens* e *Xinjianchelys levensis*, but other *Xinjianchelys* in Evers, Barret, & Benson (2019) are not. Because *Xinjianchelys* is monophyletic in Pérez-García, Gasulla, Ortega (2014) (if *Larachelus* and *Brodiechelys* are included), we assume the Evers, Barret, & Benson (2019)'s topology includes only taxa from this clade (i.e., clade that includes *Xinjianchelys*, *Larachelus* e *Brodiechelys*, but not *Protoxinjiangchelys* or *Tienfuchelys*), thus the relationship between other xinjiangchelidids follow Pérez-García, Gasulla, Ortega (2014).

-SINEMYDIDAE: Shao, Li, Yang, & Zhou (2018); Evers & Benson (2019).

**Hoyasemys jimenezi*: according to Pérez-García, de la Fuente, & Ortega (2012).

* *Galvechelone lopezmartinezae*: according to Pérez-García & Murelaga (2012).

- ANGOLACHELONIA: Evers, Barret, & Benson (2019).

-THALASSOCHELYDIA: Anquetin, Püntener, & Joyce (2017).

* In St18 *Santanachelys* is included within Eurysternidae.

- SANDOWNIDAE: Evers, Barret, & Benson (2019).

- PLATYCHELYIDAE: López-Conde, Sterli, Alvarado-Ortega, & Chavarría-Arellano (2017).

- DORTOKIDAE: Cadena & Joyce (2015).

- PAN-CHELIDAE: Holley, Sterli, & Basso (2020) and Pereira, Sterli, Moreira, & Schrago (2017).

* *Linderochelys* and *Salamanchelys*: according to Hermanson, et al. (2020).

* *Yaminuechelys sulcipeculiaris*: according to Oriozabala, Sterli, & de la Fuente (2020).

- PELOMEDUSIDAE: Pereira, Sterli, Moreira, & Schrago (2017) and Petzold, et al (2014).

-PAN-PODOCNEMIDIDAE: Hermanson, et al. (2020).

-ADOCIDAE: Syromyatnikova & Danilov (2013).

**Adocus inexpectatus*: according to Danilov, et al. (2013).

-NANHSIUNGCHELYIDAE: Tong & Li (2019).

**Basilemys gaffney*, *Basilemys morriensis* and *Zangerlia testudinomorpha*: Mallon & Brinkman (2018).

-PAN-CARETTOCHELYS: Havlik, Joyce, & Böhme (2014).

-TRIONYCHIA: Pereira, Sterli, Moreira, & Schrago (2017), Brinkman et al. (2017; implied weighting tree); other added according to: Vitek & Joyce (2015) and Georgalis & Joyce (2017).

* Plastomenidae according to Joyce, Lyson, & Sertich (2018).

* *Axestemys* according to Vitek & Joyce (2015).

* *Apalone amorensis*: according to Valdes, Bourque, & Vitek (2017).

* *Aspideretoides foveatus* and *Gobiapalone orlovi*: according to Brinkman, Rabi, & Zhou (2017).

-PAN-TESTUDINOIDEA: Vlachos (2018) and Pereira, Sterli, Moreira, & Schrago (2017) (general topology).

Pan-Emididae: Vlachos (2018); Pereira, Sterli, Moreira, & Schrago (2017).

*Polytomy within *Pseudemys*, *Graptemys* and *Trachemys*

Pan-Geoemydidae: Vlachos (2018); Pereira, Sterli, Moreira, & Schrago (2017).

**Banhxeochelys* and *Guangdongemys* according to Garbin, Böhme, & Joyce (2019).

**Hardella siamensis*: according to Claude, Suteethorn, & Tong (2007).

**Pangshura tatroia*: according to Joyce & Lyson (2010).

Pan-Testudinidae: Vlachos & Rabi (2018), Vlachos (2018), and Pereira, Sterli, Moreira, & Schrago (2017).

*Extant taxa were included following Pereira, Sterli, Moreira, & Schrago (2017); extinct taxa were positioned according to Vlachos & Rabi (2018) and Vlachos (2018).

* *Gopherus*: Vlachos (2018).

* Polytomy within *Chelonoidis*

Geochelona: Pereira, Sterli, Moreira, & Schrago (2017), Vlachos & Rabi (2018), Pérez-García, Vlachos, & Murelaga (2020).

Pan-Testudona: Vlachos & Tsoukala (2016)

**Impregnochelys* and *Gigantochersina*: according to Pérez-García, Vlachos, & Murelaga (2020).

-PAN-CHELYDRIDAE: Joyce (2016)

-PAN-KINOSTERNOIDEA: Joyce & Bourque (2016)

**Kinosternon*: polytomy (we added taxa from Pereira, Sterli, Moreira, & Schrago (2017)'s topology).

**Yelmochelys rosarioae*: according to Brinkman, Aguillon-Martinez, Hutchison, Brown (2016).

**Lutemys warren*: according to Lyson, Joyce, & Sertich (2017).

* Kinosterninae: Joyce & Bourque (2016).

-PAN-CHELONIOIDEA: Gentry, Ebersole, & Kiernan (2019), and Evers, Barret, & Benson (2019).

**Mexichelys*, *Argillochelys antiqua* and *Procolpochelys*: according to Zvonok & Danilov (2017).

Prionocheilus*, *Euclastes wielandi* , *Asmodochelys*: according to Gentry, Ebersole, & Kiernan (2019).

**Osonachelus decorata*: according to Lapparent de Broin, Murelaga, Farrés, & Altimiras (2014).

**Allopleuron qazaqstanense* and *Allopleuron lipsiensis* according to Karl, Gröning, & Brauckmann (2012).

**Rhinochelys amaberti* according to Scavezzoni & Fischer (2018).

*Ctenochelyidae: Evers, Barret, & Benson (2019).

**Santanachelys*: Protostegidae, according to Gentry, Ebersole, & Kiernan (2019) Evers, Barret, & Benson (2019), and Scavezzoni & Fisher (2018), closely related to *Solnhofia* (Thalassochelyidae according to Anquetin, Püntener, & Joyce, 2017 and Evers, Barret, & Benson, 2019), Protostegidae become more basal, within Thalassochelyidae.

* The position of Cheloniidae and Ctenochelyidae according to Evers, Barret, & Benson (2019).

**Carolinochelys* and *Trachyaspis* closely related to Cheloniidae is supported by Weems & Brown (2014) and Zvonok & Danilov (2017).

* *Pacifichelys*, *Erquelinnesia*, *Tasbacka* spp., “*Argillochelys*” *africana* and *Euclastes* is supported partially by Weems & Brown (2014) and based on Zvonok & Danilov (2017).

* Lophochelyinae as sister group of those groups, excluding *Toxochelys*, and *Mexichelys* is supported by Parham & Pyenson (2010), Weems & Brown (2014) and Zvonok & Danilov (2017).

Appendix 2 and 3 – R scripts and body size dataset

<https://github.com/BrunaFarina/Disserta-o-Bruna-Farina.git>

Appendix 4 - Summary of age median, minimum and maximum calibration dates for different clades

	“Ev19” supertree			“St18” supertree		
	Age Median	95% HPD lower	95% HPD upper	Age Median	95% HPD lower	95% HPD upper
Testudinata	238.5716	230.5678	248.2899	238.7079	232.5052	248.1817
Australochelyidae	218.655	209.2354	228.3799	230.3511	217.5963	239.8175
Helochelydridae	144.2373	134.1757	159.0412	147.843	136.6148	161.8896
Meiolaniformes	129.5019	114.8824	147.919	129.3951	119.9683	141.9348
Meiolanidae	58.8157	45.9987	69.0334	60.3703	46.4777	74.7738
Sichuanchelyidae	174.4577	165.028	189.1239	173.0536	165.3391	201.72
Paracryptodira	178.59	169.9451	193.0768	183.2329	171.31	197.8187
Baenidae	140.2908	118.8886	168.5412	140.1843	123.6151	165.626
Pleurosternidae	163.5427	156.3497	175.2561	169.3327	160.1377	177.8695
Sinemyd-	167.4941	158.6929	179.2603	169.719	157.3936	180.4845
/Macrobaenidae						
Sandownidae	140.4696	122.2643	169.5593	147.5412	123.3811	172.1027

Angolachelonia	176.3381	168.5141	182.8733	189.5656	178.9101	198.7733
Xinjiangchelyidae	178.6351	171.1946	189.9133	178.1044	171.1382	187.8746
Testudines	180.5848	171.0987	188.3373	178.3278	168.1905	189.9195
Pan-Pleurodira	172.6647	162.778	180.6892	168.2086	160.9946	182.1724
Pleurodira	155.2975	144.3835	158.1477	148.3446	134.6679	162.1753
Chelidae	126.245	112.2323	142.612	126.0781	118.1955	134.476
Pelomedusoides	153.8236	137.2292	158.1342	141.559	130.3295	153.2549
Pelomedusidae	28.1939	14.4083	52.9584	21.7268	8.115	51.8171
Bothremydidae	120.8012	113.6924	129.8172	118.9376	111.4272	126.9812
Podocnemididae	77.6581	69.7816	88.7045	83.5438	73.1053	97.915
Podocnemidinae	69.5755	58.171	78.5192	72.0781	61.4555	93.3196
Erymnochelyinae	71.7347	61.5839	80.572	76.0137	63.3622	89.4602
Cryptodira	170.8373	157.0601	181.6368	169.6707	160.8975	184.0631
Pan-Cryptodira	-	-	-	-	-	-
Trionychia	148.898	130.2043	170.8084	140.8892	125.696	155.9132

Carettochelyidae	122.8889	105.7397	144.5288	124.7168	103.4163	141.7151
Trionychidae	84.0968	69.69	105.9358	86.0023	69.7675	105.2895
Adocidae	152.6055	145.3726	160.3357	151.4987	146.1485	159.3186
Nanhsiungchelyidae	117.6053	104.899	144.3682	122.4681	108.3044	148.1324
Durocryptodira	156.8027	133.3416	173.4634	148.9329	137.5414	171.62
Pan-Chelonioidea	135.4502	115.4917	146.3869	135.8879	124.457	144.5613
Protostegidae	127.1613	113.0765	137.9536	126.1628	119.3141	134.0035
Chelonioidea	111.0734	98.4377	122.9749	118.4956	97.6767	131.0991
Dermochelyidae	95.375	80.1012	111.6066	96.731	78.5026	119.489
Cheloniidae	21.1489	3.5876	41.992	31.2914	2.7665	68.8425
Americhelyidia	142.6378	122.7681	157.3462	141.672	133.2584	160.8086
Chelydroidea	104.8738	83.0615	126.5417	110.9805	94.0852	127.509
Pan-Chelydridae	78.4723	64.0366	102.2653	84.0171	66.3303	106.0619
Chelydridae	33.8664	23.642	43.7062	36.4707	18.3973	57.4375
Kinosternoidea	81.8634	71.391	97.5452	79.4497	71.1508	89.012

Dermatemydidae	76.1589	69.0754	89.4618	76.6101	69.6066	84.3461
Pan-Kinosternidae	-	-	-	-	-	-
Kinosternidae	70.8271	55.7707	80.1151	68.9272	58.6717	8964
Testudinoidea	88.4827	66.2771	127.9402	102.9054	82.0062	125.4088
Testuguria	79.9064	60.529	96.879	86.361	73.6207	103.5057
Testudinidae	62.0803	45.7094	71.4445	61.2453	48.8408	76.8357
Geoemydidae	73.4546	57.8996	87.0246	73.7679	65.6478	90.8283
Emysternia	72.135	58.0678	105.8703	72.7776	59.084	91.0947
Platysternidae	-	-	-	62.919	51.7248	77.3899
Emydidae	62.0923	51.7648	82.9868	64.3484	52.1786	77.8689
